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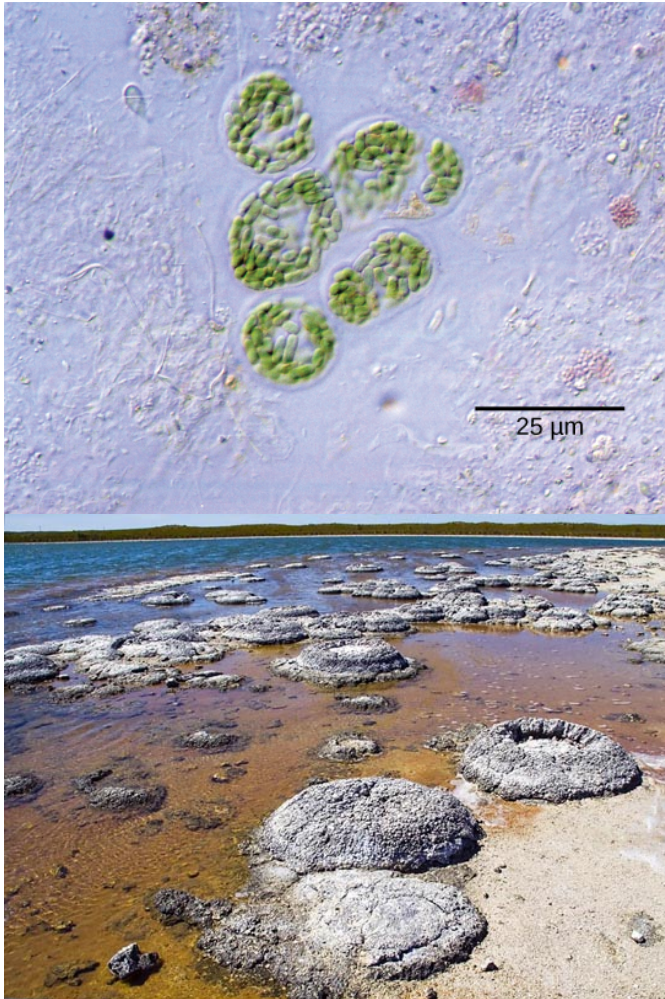
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The Science of Biology

By the end of this section, you will be able to:

- Identify the shared characteristics of the natural sciences
- Summarize the steps of the scientific method
- Compare inductive reasoning with deductive reasoning
- Describe the goals of basic science and applied science

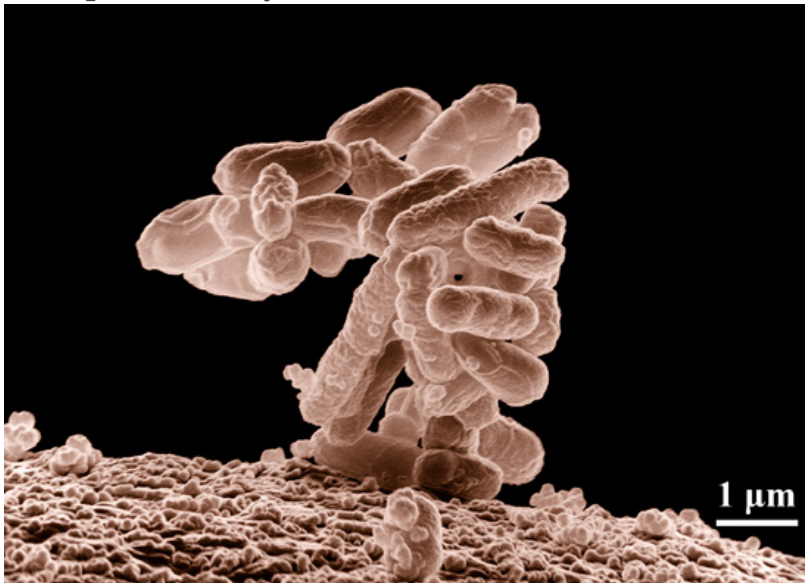
Formerly called blue-green algae, these (a) cyanobacteria, shown here at 300x magnification under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)



What is biology? In simple terms, **biology** is the study of living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of biology is vast. Biologists may study anything from the microscopic or submicroscopic view of a cell to ecosystems and the whole living planet ([\[link\]](#)). Listening to the daily news, you will quickly realize

how many aspects of biology are discussed every day. For example, recent news topics include *Escherichia coli* ([\[link\]](#)) outbreaks in spinach and *Salmonella* contamination in peanut butter. Other subjects include efforts toward finding a cure for AIDS, Alzheimer's disease, and cancer. On a global scale, many researchers are committed to finding ways to protect the planet, solve environmental issues, and reduce the effects of climate change. All of these diverse endeavors are related to different facets of the discipline of biology.

Escherichia coli (*E. coli*) bacteria, seen in this scanning electron micrograph, are normal residents of our digestive tracts that aid in the absorption of vitamin K and other nutrients. However, virulent strains are sometimes responsible for disease outbreaks. (credit: Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU)



The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields.
(credit: “Image Editor”/Flickr)

The Process of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? **Science** (from the Latin *scientia*, meaning “knowledge”) can be defined as knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method. It becomes clear from this definition that the application of the scientific method plays a major role in science. The **scientific method** is a method of research with defined steps that include experiments and careful observation.

The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses by means of repeatable experiments. A **hypothesis** is a suggested explanation for an event, which can be tested. Although using the scientific method is inherent to science, it is inadequate in determining what science is. This is because it is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but when it comes to disciplines like archaeology, psychology, and

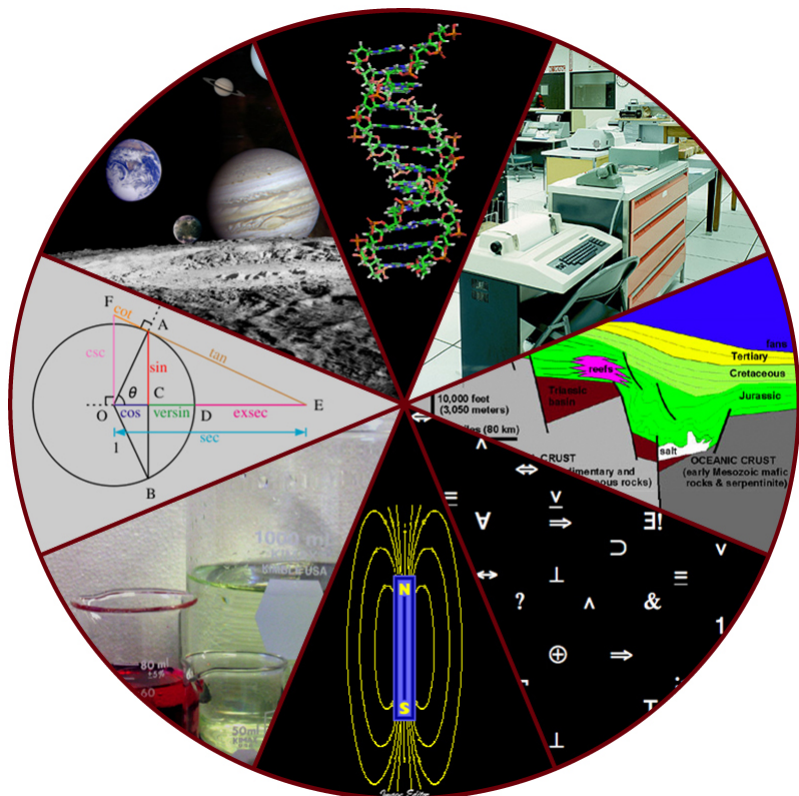
geology, the scientific method becomes less applicable as it becomes more difficult to repeat experiments.

These areas of study are still sciences, however. Consider archeology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, an archeologist can hypothesize that an ancient culture existed based on finding a piece of pottery. Further hypotheses could be made about various characteristics of this culture, and these hypotheses may be found to be correct or false through continued support or contradictions from other findings. A hypothesis may become a verified theory. A **theory** is a tested and confirmed explanation for observations or phenomena. Science may be better defined as fields of study that attempt to comprehend the nature of the universe.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or, maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics ([\[link\]](#)). However, those fields of science related to the physical world and its phenomena and processes are

considered **natural sciences**. Thus, a museum of natural sciences might contain any of the items listed above.



There is no complete agreement when it comes to defining what the natural sciences include, however. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into **life sciences**, which study living things and include biology, and **physical sciences**, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some

disciplines such as biophysics and biochemistry build on both life and physical sciences and are interdisciplinary. Natural sciences are sometimes referred to as “hard science” because they rely on the use of quantitative data; social sciences that study society and human behavior are more likely to use qualitative assessments to drive investigations and findings.

Not surprisingly, the natural science of biology has many branches or subdisciplines. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals.

Scientific Reasoning

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking

that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative or quantitative, and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies provide an example. In this type of research, many live brains are observed while people are doing a specific activity, such as viewing images of food. The part of the brain that “lights up” during this activity is then predicted to be the part controlling the response to the selected stimulus, in this case, images of food. The “lighting up” of the various areas of the brain is caused by excess absorption of radioactive sugar derivatives by active areas of the brain. The resultant increase in radioactivity is observed by a scanner. Then, researchers can stimulate that part of the brain to see if similar responses result.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reason, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. **Deductive reasoning** is a form of logical thinking that uses a general principle or law to

forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. **Descriptive (or discovery) science**, which is usually inductive, aims to observe, explore, and discover, while **hypothesis-based science**, which is usually deductive, begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, and most scientific endeavors combine both approaches. The fuzzy boundary becomes apparent when thinking about how easily observation can lead to specific questions. For example, a gentleman in the 1940s observed that the burr seeds that stuck to his clothes and his dog's fur had a tiny hook structure. On closer inspection, he discovered that the burrs' gripping device was more reliable than a zipper. He eventually

developed a company and produced the hook-and-loop fastener popularly known today as Velcro. Descriptive science and hypothesis-based science are in continuous dialogue.

Sir Francis Bacon (1561–1626) is credited with being the first to define the scientific method.
(credit: Paul van Somer)

The Scientific Method

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) ([\[link\]](#)), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method.



The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Proposing a Hypothesis

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, the student can make a prediction. A prediction is similar to a hypothesis but it typically has the format “If . . . then” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

Testing a Hypothesis

A valid hypothesis must be testable. It should also be **falsifiable**, meaning that it can be disproven by experimental results. Importantly, science does not claim to “prove” anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural,

for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. The **control group** contains every feature of the experimental group except it is not given the manipulation that is hypothesized about. Therefore, if the results of the experimental group differ from the control group, the difference must be due to the hypothesized manipulation, rather than some outside factor. Look for the variables and controls in the examples that follow. To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure and this hypothesis should be rejected. Each hypothesis should be tested by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid ([\[link\]](#)). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this “warm classroom” example is based on

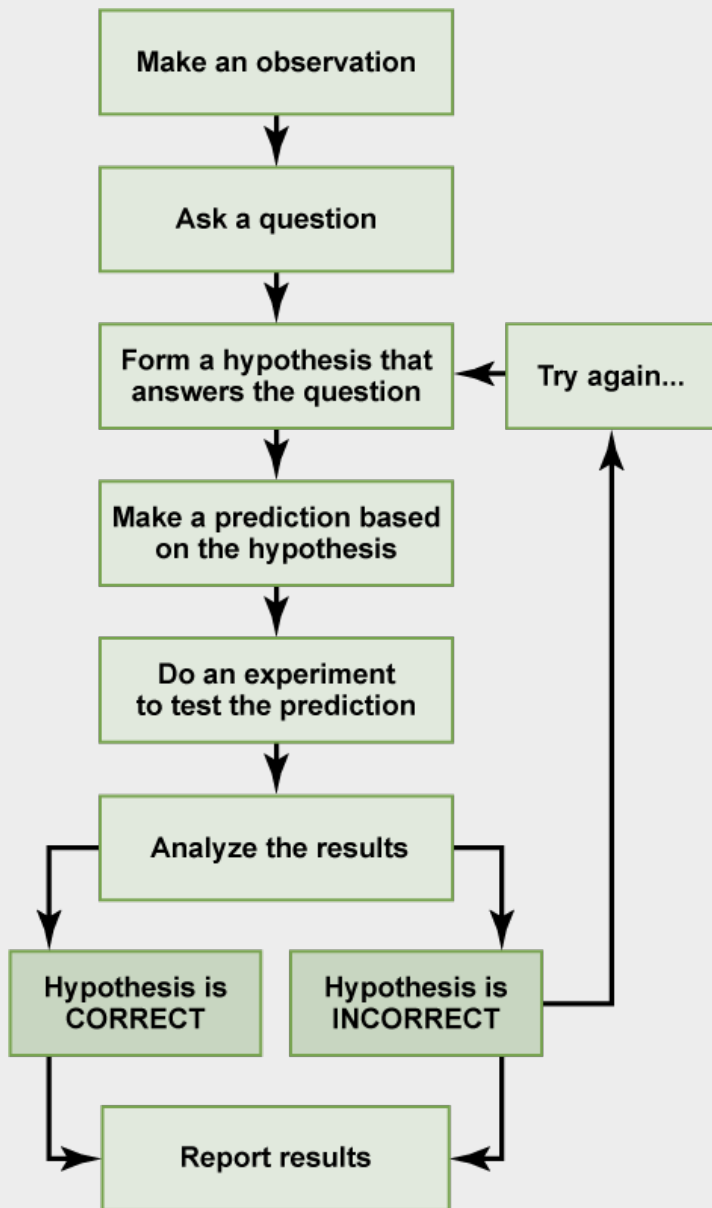
observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One observation to explain this occurrence might be, “When I eat breakfast before class, I am better able to pay attention.” The student could then design an experiment with a control to test this hypothesis.

In hypothesis-based science, specific results are predicted from a general premise. This type of reasoning is called deductive reasoning: deduction proceeds from the general to the particular. But the reverse of the process is also possible: sometimes, scientists reach a general conclusion from a number of specific observations. This type of reasoning is called inductive reasoning, and it proceeds from the particular to the general. Inductive and deductive reasoning are often used in tandem to advance scientific knowledge ([\[link\]](#)). In recent years a new approach of testing hypotheses has developed as a result of an exponential growth of data deposited in various databases. Using computer algorithms and statistical analyses of data in databases, a new field of so-called "data research" (also referred to as "in silico" research) provides new methods of data analyses and their interpretation. This will increase the demand for specialists in both biology and computer science, a promising career opportunity.

Art Connection

The scientific method consists of a series of well-defined steps. If a hypothesis is not supported by experimental data, a new hypothesis can be proposed.

Make an observation



In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items).

Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

1. There is something wrong with the electrical outlet.
2. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
3. My toaster doesn't toast my bread.
4. I plug my coffee maker into the outlet.
5. My coffeemaker works.
6. Why doesn't my toaster work?

Art Connection

Scientists use two types of reasoning, inductive and deductive reasoning, to advance scientific knowledge. As is the case in this example, the conclusion from inductive reasoning can often become the premise for inductive reasoning.

Two Types of Reasoning

Inductive reasoning:

from a number of observations, a general conclusion is drawn.

Observations

- Members of a species are not all the same.
- Individuals compete for resources.
- Species are generally adapted to their environment.



Conclusion

Individuals most adapted to their environment are more likely to survive and pass their traits to the next generation.

Deductive reasoning:

from a general premise, specific results are predicted.

General premise

Individuals most adapted to their environment are more likely to survive and pass their traits on to the next generation.



Predicted results

If the average temperature in an ecosystem increases due to climate change, individuals better adapted to warmer temperatures will outcompete those that are not.

Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will

become more problematic if global temperatures increase.

3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

The scientific method may seem too rigid and structured. It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

After Hurricane Ike struck the Gulf Coast in 2008, the U.S. Fish and Wildlife Service rescued this brown pelican. Thanks to applied science, scientists knew how to rehabilitate the bird. (credit: FEMA)

The Human Genome Project was a 13-year

collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003. (credit: the U.S. Department of Energy Genome Programs (<http://genomics.energy.gov>))

Two Types of Science: Basic Science and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or to bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge’s sake, though this does not mean that, in the end, it may not result in a practical application.

In contrast, **applied science** or “technology,” aims to use science to solve real-world problems, making

it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster ([\[link\]](#)). In applied science, the problem is usually defined for the researcher.



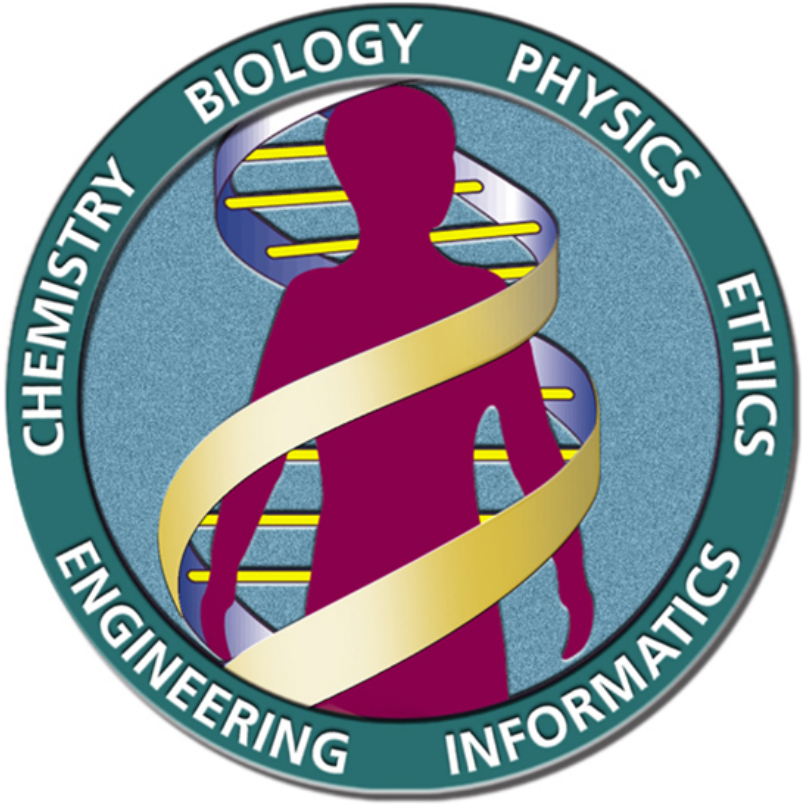
Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems.

Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the wide knowledge foundation generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, DNA makes new copies of itself, shortly before a cell divides. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual's complete collection of genes is his or her genome.) Other less complex organisms have also been studied as part of this project in order to

gain a better understanding of human chromosomes. The Human Genome Project ([\[link\]](#)) relied on basic research carried out with simple organisms and, later, with the human genome. An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.



While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by **serendipity**, that is, by means of a fortunate accident or a lucky surprise. Penicillin was

discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew on the dish, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. **Peer-reviewed manuscripts** are scientific papers that are reviewed by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The

process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. First, scientific writing must be brief, concise, and accurate. A scientific paper needs to be succinct but detailed enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections—introduction, materials and methods, results, and discussion. This structure is sometimes called the “IMRaD” format. There are usually acknowledgment and reference sections as well as an **abstract** (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The **introduction** starts with brief, but broad,

background information about what is known in the field. A good introduction also gives the rationale of the work; it justifies the work carried out and also briefly mentions the end of the paper, where the hypothesis or research question driving the research will be presented. The introduction refers to the published scientific work of others and therefore requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered **plagiarism**.

The **materials and methods** section includes a complete and accurate description of the substances used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Some journals require a results section followed by a discussion section, but it is more common to combine both. If the journal does not allow the combination of both sections, the **results** section simply narrates the findings without any further interpretation. The results are presented by means

of tables or graphs, but no duplicate information should be presented. In the **discussion** section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously published scientific research. Therefore, proper citations are included in this section as well.

Finally, the **conclusion** section summarizes the importance of the experimental findings. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. Therefore, a well-done scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRAD format because they do not present original scientific findings, or primary literature; instead, they summarize and comment on findings that were published as primary literature and typically include extensive reference sections.

Section Summary

Biology is the science that studies living organisms and their interactions with one another and their

environments. Science attempts to describe and understand the nature of the universe in whole or in part by rational means. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Two types of logical reasoning are used in science. Inductive reasoning uses particular results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method, a step-based process that consists of making observations, defining a problem, posing hypotheses, testing these hypotheses, and drawing one or more conclusions. The testing uses proper controls. Scientists present their results in peer-reviewed scientific papers published in scientific journals. A scientific research paper consists of several well-defined sections: introduction, materials and methods, results, and, finally, a concluding discussion. Review papers summarize the research done in a particular field over a period of time.

Art Connections

[\[link\]](#) In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

1. Observation
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 3. Hypothesis (answer)
 4. Prediction
 5. Experiment
 6. Result
-
1. There is something wrong with the electrical outlet.
 2. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
 3. My toaster doesn't toast my bread.
 4. I plug my coffee maker into the outlet.
 5. My coffeemaker works.
 6. Why doesn't my toaster work?

[\[link\]](#) 1: C; 2: F; 3: A; 4: B; 5: D; 6: E. The original hypothesis is incorrect, as the

coffeemaker works when plugged into the outlet. Alternative hypotheses include that the toaster might be broken or that the toaster wasn't turned on.

[\[link\]](#) Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will become more problematic if global temperatures increase.
3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

[\[link\]](#) 1: inductive; 2: deductive; 3: deductive; 4: inductive.

Review Questions

The first forms of life on Earth were _____.

1. plants
 2. microorganisms
 3. birds
 4. dinosaurs
-

B

A suggested and testable explanation for an event is called a _____.

1. hypothesis
 2. variable
 3. theory
 4. control
-

A

Which of the following sciences is not considered a natural science?

1. biology
2. astronomy
3. physics

4. computer science

D

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

1. deductive reasoning
 2. the scientific method
 3. hypothesis-based science
 4. inductive reasoning
-

D

The process of _____ helps to ensure that a scientist's research is original, significant, logical, and thorough.

1. publication
 2. public speaking
 3. peer review
 4. the scientific method
-

C

A person notices that her houseplants that are regularly exposed to music seem to grow more quickly than those in rooms with no music. As a result, she determines that plants grow better when exposed to music. This example most closely resembles which type of reasoning?

1. inductive reasoning
2. deductive reasoning
3. neither, because no hypothesis was made
4. both inductive and deductive reasoning

A

Free Response

Although the scientific method is used by most of the sciences, it can also be applied to everyday situations. Think about a problem that you may have at home, at school, or with your car, and apply the scientific method to solve it.

Answers will vary, but should apply the steps of the scientific method. One possibility could be a car which doesn't start. The hypothesis could be that the car doesn't start because the battery is

dead. The experiment would be to change the battery or to charge the battery and then check whether the car starts or not. If it starts, the problem was due to the battery, and the hypothesis is accepted.

Give an example of how applied science has had a direct effect on your daily life.

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such as polio, measles, tetanus, and even influenza affect daily life by contributing to individual and societal health.

Name two topics that are likely to be studied by biologists, and two areas of scientific study that would fall outside the realm of biology.

Answers will vary. Topics that fall inside the area of biological study include how diseases affect human bodies, how pollution impacts a species' habitat, and how plants respond to their environments. Topics that fall outside of biology (the "study of life") include how metamorphic rock is formed and how planetary orbits function.

Thinking about the topic of cancer, write a basic science question and an applied science question that a researcher interested in this topic might ask

Answers will vary. Basic science: What evolutionary purpose might cancer serve?
Applied science: What strategies might be found to prevent cancer from reproducing at the cellular level?

Glossary

abstract

opening section of a scientific paper that summarizes the research and conclusions

applied science

form of science that aims to solve real-world problems

basic science

science that seeks to expand knowledge and understanding regardless of the short-term application of that knowledge

biology

the study of living organisms and their interactions with one another and their environments

conclusion

section of a scientific paper that summarizes the importance of the experimental findings

control

part of an experiment that does not change during the experiment

deductive reasoning

form of logical thinking that uses a general inclusive statement to forecast specific results

descriptive science

(also, discovery science) form of science that aims to observe, explore, and investigate

discussion

section of a scientific paper in which the author interprets experimental results, describes how variables may be related, and attempts to explain the phenomenon in question

falsifiable

able to be disproven by experimental results

hypothesis

suggested explanation for an observation, which can be tested

hypothesis-based science

form of science that begins with a specific

question and potential testable answers

inductive reasoning

form of logical thinking that uses related observations to arrive at a general conclusion

introduction

opening section of a scientific paper, which provides background information about what was known in the field prior to the research reported in the paper

life science

field of science, such as biology, that studies living things

materials and methods

section of a scientific paper that includes a complete description of the substances, methods, and techniques used by the researchers to gather data

natural science

field of science that is related to the physical world and its phenomena and processes

peer-reviewed manuscript

scientific paper that is reviewed by a scientist's colleagues who are experts in the field of study

physical science

field of science, such as geology, astronomy, physics, and chemistry, that studies nonliving matter

plagiarism

using other people's work or ideas without proper citation, creating the false impression that those are the author's original ideas

results

section of a scientific paper in which the author narrates the experimental findings and presents relevant figures, pictures, diagrams, graphs, and tables, without any further interpretation

review article

paper that summarizes and comments on findings that were published as primary literature

science

knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific method

method of research with defined steps that include observation, formulation of a hypothesis, testing, and confirming or falsifying the hypothesis

serendipity

fortunate accident or a lucky surprise

theory

tested and confirmed explanation for
observations or phenomena

variable

part of an experiment that the experimenter
can vary or change

Themes and Concepts of Biology

By the end of this section, you will be able to:

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Recognize and interpret a phylogenetic tree
- List examples of different sub disciplines in biology

Biology is the science that studies life, but what exactly is life? This may sound like a silly question with an obvious response, but it is not always easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life. Consequently, virologists are not biologists, strictly speaking. Similarly, some biologists study the early molecular evolution that gave rise to life; since the events that preceded life are not biological events, these scientists are also excluded from biology in the strict sense of the term.

From its earliest beginnings, biology has wrestled with three questions: What are the shared properties that make something “alive”? And once we know something is alive, how do we find meaningful

levels of organization in its structure? And, finally, when faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? As new organisms are discovered every day, biologists continue to seek answers to these and other questions.

A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: “Ivengo”/Wikimedia Commons) The leaves of this sensitive plant (*Mimosa pudica*) will instantly droop and fold when touched. After a few minutes, the plant returns to normal. (credit: Alex Lomas) Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Rocky Mountain Feline Rescue) Polar bears (*Ursus maritimus*) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: “longhorndave”/Flickr) The California condor (*Gymnogyps californianus*) uses chemical energy derived from food to power flight. California condors are an endangered species; this bird has a wing tag that helps biologists identify the individual. (credit: Pacific Southwest Region U.S. Fish and Wildlife Service)

Properties of Life

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation, homeostasis, energy processing, and evolution. When viewed together, these nine characteristics serve to define life.

Order



Organisms are highly organized, coordinated structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex: inside each cell, atoms make up molecules; these in turn make up cell organelles and other cellular inclusions. In multicellular organisms ([\[link\]](#)), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form

organ systems.

Sensitivity or Response to Stimuli



Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch ([\[link\]](#)). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light (*phototaxis*). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



Watch [this video](#) to see how plants respond to a stimulus—from opening to light, to wrapping a tendril around a branch, to capturing prey.

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline cells that will form new individuals. When reproduction occurs, genes containing DNA are passed along to an organism's offspring. These genes ensure that the offspring will belong to the same species and will have similar characteristics, such as size and shape.

Growth and Development

Organisms grow and develop following specific instructions coded for by their genes. These genes

provide instructions that will direct cellular growth and development, ensuring that a species' young ([\[link\]](#)) will grow up to exhibit many of the same characteristics as its parents.



Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. Organs (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis



In order to function properly, cells need to have appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through **homeostasis** (literally, “steady state”)—the ability of an organism to maintain constant internal conditions. For example, an organism needs to regulate body temperature through a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear ([\[link\]](#)), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or

panting in dogs) that help them to shed excess body heat.

Energy Processing



All organisms use a source of energy for their metabolic activities. Some organisms capture energy from the sun and convert it into chemical energy in food; others use chemical energy in molecules they take in as food ([\[link\]](#)).

All molecules, including this DNA molecule, are

composed of atoms. (credit: “brian0918”/Wikimedia Commons)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy that can be examined on a scale from small to large. The **atom** is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A **molecule** is a chemical structure consisting of at least two atoms held together by one or more chemical bonds. Many molecules that are biologically important are **macromolecules**, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA) ([\[link\]](#)), which contains the instructions for the structure and functioning of all living organisms.



Link to Learning



Watch [this video](#) that animates the three-dimensional structure of the DNA molecule shown in [\[link\]](#).

Some cells contain aggregates of macromolecules surrounded by membranes; these are called **organelles**. Organelles are small structures that exist within cells. Examples of organelles include mitochondria and chloroplasts, which carry out indispensable functions: mitochondria produce energy to power the cell, while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of cells; the **cell** itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack the reproductive mechanism of a living cell; only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell

and others are multicellular. Cells are classified as prokaryotic or eukaryotic. **Prokaryotes** are single-celled or colonial organisms that do not have membrane-bound nuclei; in contrast, the cells of **eukaryotes** do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make **tissues**, which are groups of similar cells carrying out similar or related functions. **Organs** are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An **organ system** is a higher level of organization that consists of functionally related organs. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs; it includes organs such as the heart and blood vessels. **Organisms** are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

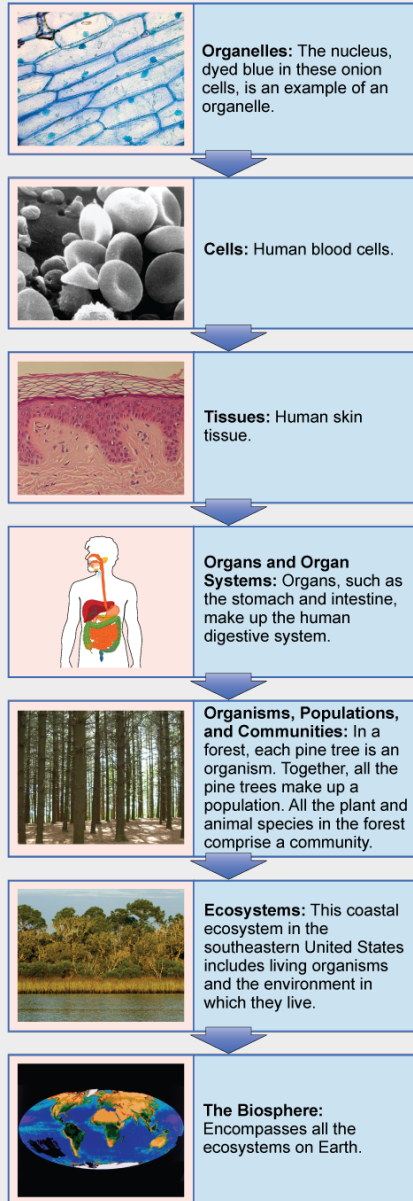
All the individuals of a species living within a specific area are collectively called a **population**. For example, a forest may include many pine trees. All of these pine trees represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of

flowering plants and also insects and microbial populations. A **community** is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An **ecosystem** consists of all the living things in a particular area together with the abiotic, non-living parts of that environment such as nitrogen in the soil or rain water. At the highest level of organization ([\[link\]](#)), the **biosphere** is the collection of all ecosystems, and it represents the zones of life on earth. It includes land, water, and even the atmosphere to a certain extent.

Art Connection

The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit "organelles": modification of work by Umberto Salvagnin; credit "cells": modification of work by Bruce Wetzell, Harry Schaefer/ National Cancer Institute; credit "tissues": modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit "organs": modification of work by Mariana Ruiz Villareal; credit "organisms": modification of work by "Crystal"/Flickr; credit "ecosystems": modification of work by US Fish and Wildlife Service)

Headquarters; credit “biosphere”: modification of work by NASA)



Which of the following statements is false?

1. Tissues exist within organs which exist within organ systems.
2. Communities exist within populations which exist within ecosystems.
3. Organelles exist within cells which exist within tissues.
4. Communities exist within ecosystems which exist in the biosphere.

This phylogenetic tree was constructed by microbiologist Carl Woese using data obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

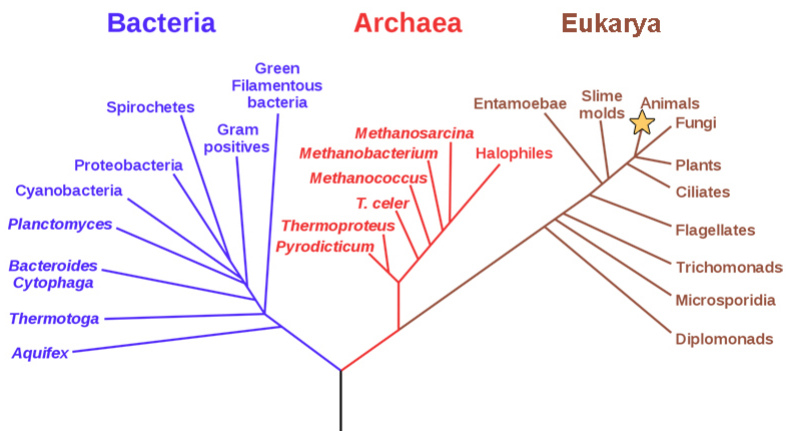
The Diversity of Life

The fact that biology, as a science, has such a broad scope has to do with the tremendous diversity of life on earth. The source of this diversity is **evolution**, the process of gradual change during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

The evolution of various life forms on Earth can be summarized in a phylogenetic tree ([\[link\]](#)). A **phylogenetic tree** is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of nodes and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.

Phylogenetic Tree of Life

★ = You are here



Evolution Connection

Carl Woese and the Phylogenetic Tree

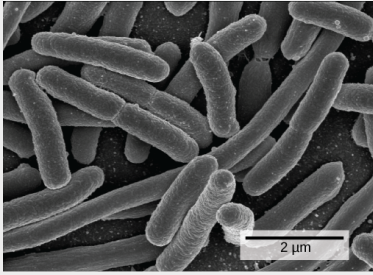
In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists,

and bacteria. The organizational scheme was based mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which are used by modern systematics. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms together with the four original kingdoms (excluding bacteria). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree ([\[link\]](#)). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape).

Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparisons of physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic

variability ([\[link\]](#)). The comparison of homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified the separation of the prokaryotes into two domains: bacteria and archaea.

These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work by Drew March; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Leszek Leszczynski)



(a)



(b)



(c)



(d)

Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a more focused field. For instance, **molecular biology** and **biochemistry** study biological processes at the

molecular and chemical level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated.

Microbiology, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Career Connection

Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace materials associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have expanded the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA ([\[link\]](#)) found in many different

environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect larvae or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.

This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA. (credit: United States Army CID Command Public Affairs)



Another field of biological study, **neurobiology**, studies the biology of the nervous system, and although it is considered a branch of biology, it is also recognized as an interdisciplinary field of study known as neuroscience. Because of its

interdisciplinary nature, this subdiscipline studies different functions of the nervous system using molecular, cellular, developmental, medical, and computational approaches.



Paleontology, another branch of biology, uses fossils to study life's history ([\[link\]](#)). **Zoology** and **botany** are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. This is just a small sample of the many fields that biologists can pursue.

Biology is the culmination of the achievements of the natural sciences from their inception to today. Excitingly, it is the cradle of emerging sciences, such as the biology of brain activity, genetic engineering of custom organisms, and the biology of evolution

that uses the laboratory tools of molecular biology to retrace the earliest stages of life on earth. A scan of news headlines—whether reporting on immunizations, a newly discovered species, sports doping, or a genetically-modified food—demonstrates the way biology is active in and important to our everyday world.

Section Summary

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized parts of a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. Organisms, in turn, are grouped as populations, communities, ecosystems, and the biosphere. The great diversity of life today evolved from less-diverse ancestral organisms over billions of years. A diagram called a phylogenetic tree can be used to show evolutionary relationships among organisms.

Biology is very broad and includes many branches and subdisciplines. Examples include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

Art Connections

[\[link\]](#) Which of the following statements is false?

1. Tissues exist within organs which exist within organ systems.
 2. Communities exist within populations which exist within ecosystems.
 3. Organelles exist within cells which exist within tissues.
 4. Communities exist within ecosystems which exist in the biosphere.
-

[\[link\]](#) Communities exist within populations which exist within ecosystems.

Review Questions

The smallest unit of biological structure that meets the functional requirements of “living” is the _____.

1. organ
2. organelle
3. cell

4. macromolecule

C

Viruses are not considered living because they _____.

1. are not made of cells
 2. lack cell nuclei
 3. do not contain DNA or RNA
 4. cannot reproduce
-

A

The presence of a membrane-enclosed nucleus is a characteristic of _____.

1. prokaryotic cells
 2. eukaryotic cells
 3. living organisms
 4. bacteria
-

B

A group of individuals of the same species living in the same area is called a(n) _____.

1. family
 2. community
 3. population
 4. ecosystem
-

C

Which of the following sequences represents the hierarchy of biological organization from the most inclusive to the least complex level?

1. organelle, tissue, biosphere, ecosystem, population
 2. organ, organism, tissue, organelle, molecule
 3. organism, community, biosphere, molecule, tissue, organ
 4. biosphere, ecosystem, community, population, organism
-

D

Where in a phylogenetic tree would you expect to find the organism that had evolved most recently?

1. at the base
2. within the branches

3. at the nodes
4. at the branch tips

D

Free Response

Select two items that biologists agree are necessary in order to consider an organism “alive.” For each, give an example of a non-living object that otherwise fits the definition of “alive,”

Answers will vary. Layers of sedimentary rock have order but are not alive. Technology is capable of regulation but is not, of itself, alive.

Consider the levels of organization of the biological world, and place each of these items in order from smallest level of organization to most encompassing: skin cell, elephant, water molecule, planet Earth, tropical rainforest, hydrogen atom, wolf pack, liver.

Smallest level of organization to largest:

hydrogen atom, water molecule, skin cell, liver, elephant, wolf pack, tropical rainforest, planet Earth

You go for a long walk on a hot day. Give an example of a way in which homeostasis keeps your body healthy.

During your walk, you may begin to perspire, which cools your body and helps your body to maintain a constant internal temperature. You might also become thirsty and pause long enough for a cool drink, which will help to restore the water lost during perspiration.

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population's community, the community's ecosystem, and the ecosystem's part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and

their respective organ systems, and the sum total—the organism itself.

Glossary

atom

smallest and most fundamental unit of matter

biochemistry

study of the chemistry of biological organisms

biosphere

collection of all the ecosystems on Earth

botany

study of plants

cell

smallest fundamental unit of structure and function in living things

community

set of populations inhabiting a particular area

ecosystem

all the living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote

organism with cells that have nuclei and

membrane-bound organelles

evolution

process of gradual change during which new species arise from older species and some species become extinct

homeostasis

ability of an organism to maintain constant internal conditions

macromolecule

large molecule, typically formed by the joining of smaller molecules

microbiology

study of the structure and function of microorganisms

molecule

chemical structure consisting of at least two atoms held together by one or more chemical bonds

molecular biology

study of biological processes and their regulation at the molecular level, including interactions among molecules such as DNA, RNA, and proteins

neurobiology

study of the biology of the nervous system

organ

collection of related tissues grouped together performing a common function

organ system

level of organization that consists of functionally related interacting organs

organelle

small structures that exist within cells and carry out cellular functions

organism

individual living entity

paleontology

study of life's history by means of fossils

phylogenetic tree

diagram showing the evolutionary relationships among various biological species based on similarities and differences in genetic or physical traits or both; in essence, a hypothesis concerning evolutionary connections

population

all of the individuals of a species living within a specific area

prokaryote

single-celled organism that lacks organelles

and does not have nuclei surrounded by a nuclear membrane

tissue

group of similar cells carrying out related functions

zoology

study of animals

Atoms, Isotopes, Ions, and Molecules: The Building Blocks

By the end of this section, you will be able to:

- Define matter and elements
- Describe the interrelationship between protons, neutrons, and electrons
- Compare the ways in which electrons can be donated or shared between atoms
- Explain the ways in which naturally occurring elements combine to create molecules, cells, tissues, organ systems, and organisms

At its most fundamental level, life is made up of matter. **Matter** is any substance that occupies space and has mass. **Elements** are unique forms of matter with specific chemical and physical properties that cannot be broken down into smaller substances by ordinary chemical reactions. There are 118 elements, but only 92 occur naturally. The remaining elements are synthesized in laboratories and are unstable.

Each element is designated by its chemical symbol, which is a single capital letter or, when the first letter is already “taken” by another element, a combination of two letters. Some elements follow the English term for the element, such as C for carbon and Ca for calcium. Other elements’ chemical symbols derive from their Latin names; for example, the symbol for sodium is Na, referring to

natrium, the Latin word for sodium.

The four elements common to all living organisms are oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). In the non-living world, elements are found in different proportions, and some elements common to living organisms are relatively rare on the earth as a whole, as shown in [\[link\]](#). For example, the atmosphere is rich in nitrogen and oxygen but contains little carbon and hydrogen, while the earth's crust, although it contains oxygen and a small amount of hydrogen, has little nitrogen and carbon. In spite of their differences in abundance, all elements and the chemical reactions between them obey the same chemical and physical laws regardless of whether they are a part of the living or non-living world.

**Approximate
Percentage
of Elements
in Living
Organisms
(Humans)
Compared
to the Non-
living**

World Element	Life (Humans)	Atmosphere	Earth's Crust
Oxygen (O)	65%	21%	46%
Carbon (C)	18%	trace	trace
Hydrogen (H)	10%	trace	0.1%
Nitrogen (N)	3%	78%	trace

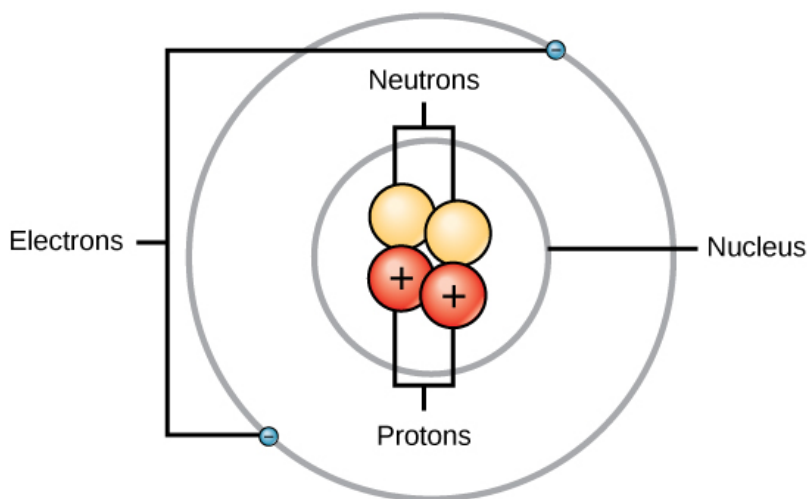
Elements, such as helium, depicted here, are made up of atoms. Atoms are made up of protons and neutrons located within the nucleus, with electrons in orbitals surrounding the nucleus.

The Structure of the Atom

To understand how elements come together, we must first discuss the smallest component or building block of an element, the atom. An **atom** is the smallest unit of matter that retains all of the chemical properties of an element. For example, one gold atom has all of the properties of gold in that it is a solid metal at room temperature. A gold coin is simply a very large number of gold atoms molded into the shape of a coin and containing small amounts of other elements known as impurities. Gold atoms cannot be broken down into anything smaller while still retaining the properties of gold.

An atom is composed of two regions: the **nucleus**, which is in the center of the atom and contains

protons and neutrons, and the outermost region of the atom which holds its electrons in orbit around the nucleus, as illustrated in [\[link\]](#). Atoms contain protons, electrons, and neutrons, among other subatomic particles. The only exception is hydrogen (H), which is made of one proton and one electron with no neutrons.



Protons and neutrons have approximately the same mass, about 1.67×10^{-24} grams. Scientists arbitrarily define this amount of mass as one atomic mass unit (amu) or one Dalton, as shown in [\[link\]](#). Although similar in mass, protons and neutrons differ in their electric charge. A **proton** is positively charged whereas a **neutron** is uncharged. Therefore, the number of neutrons in an atom contributes significantly to its mass, but not to its charge. **Electrons** are much smaller in mass than protons, weighing only 9.11×10^{-28} grams, or about 1/1800 of an atomic mass unit. Hence, they do not

contribute much to an element's overall atomic mass. Therefore, when considering atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone. Although not significant contributors to mass, electrons do contribute greatly to the atom's charge, as each electron has a negative charge equal to the positive charge of a proton. In uncharged, neutral atoms, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. In these atoms, the positive and negative charges cancel each other out, leading to an atom with no net charge.

Accounting for the sizes of protons, neutrons, and electrons, most of the volume of an atom—greater than 99 percent—is, in fact, empty space. With all this empty space, one might ask why so-called solid objects do not just pass through one another. The reason they do not is that the electrons that surround all atoms are negatively charged and negative charges repel each other.

**Protons,
Neutrons,
and
Electrons**

--	--	--	--	--

	Charge	Mass (amu)	Location
Proton	+1	1	nucleus
Neutron	0	1	nucleus
Electron	-1	0	orbitals

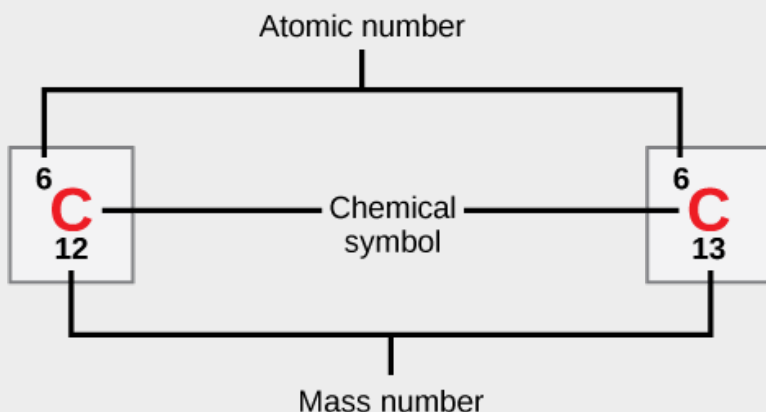
Atomic Number and Mass

Atoms of each element contain a characteristic number of protons and electrons. The number of protons determines an element's **atomic number** and is used to distinguish one element from another. The number of neutrons is variable, resulting in isotopes, which are different forms of the same atom that vary only in the number of neutrons they possess. Together, the number of protons and the number of neutrons determine an element's **mass number**, as illustrated in [\[link\]](#). Note that the small contribution of mass from electrons is disregarded in calculating the mass number. This approximation of mass can be used to easily calculate how many neutrons an element has by simply subtracting the number of protons from the mass number. Since an element's isotopes will have slightly different mass numbers, scientists also determine the **atomic mass**, which is the calculated mean of the mass number for its naturally occurring isotopes. Often, the resulting number contains a fraction. For example, the atomic mass of chlorine (Cl) is 35.45 because chlorine is composed of several isotopes, some (the

majority) with atomic mass 35 (17 protons and 18 neutrons) and some with atomic mass 37 (17 protons and 20 neutrons).

Art Connection

Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its relative atomic mass is 12.011



How many neutrons do carbon-12 and carbon-13 have, respectively?

Isotopes

Isotopes are different forms of an element that have the same number of protons but a different number

of neutrons. Some elements—such as carbon, potassium, and uranium—have naturally occurring isotopes. Carbon-12 contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12 (six protons and six neutrons).

Carbon-14 contains six protons, eight neutrons, and six electrons; its atomic mass is 14 (six protons and eight neutrons). These two alternate forms of carbon are isotopes. Some isotopes may emit neutrons, protons, and electrons, and attain a more stable atomic configuration (lower level of potential energy); these are radioactive isotopes, or **radioisotopes**. Radioactive decay (carbon-14 decaying to eventually become nitrogen-14) describes the energy loss that occurs when an unstable atom's nucleus releases radiation.

Evolution Connection

Carbon Dating

Carbon is normally present in the atmosphere in the form of gaseous compounds like carbon dioxide and methane. Carbon-14 (^{14}C) is a naturally occurring radioisotope that is created in the atmosphere from atmospheric ^{14}N (nitrogen) by the addition of a neutron and the loss of a proton because of cosmic rays. This is a continuous process, so more ^{14}C is always being created. As a living organism incorporates ^{14}C initially as carbon dioxide fixed in the process of photosynthesis, the

relative amount of ^{14}C in its body is equal to the concentration of ^{14}C in the atmosphere. When an organism dies, it is no longer ingesting ^{14}C , so the ratio between ^{14}C and ^{12}C will decline as ^{14}C decays gradually to ^{14}N by a process called beta decay—the emission of electrons or positrons. This decay gives off energy in a slow process. After approximately 5,730 years, half of the starting concentration of ^{14}C will have been converted back to ^{14}N . The time it takes for half of the original concentration of an isotope to decay back to its more stable form is called its half-life. Because the half-life of ^{14}C is long, it is used to date formerly living objects such as old bones or wood. Comparing the ratio of the ^{14}C concentration found in an object to the amount of ^{14}C detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. On the basis of this amount, the age of the material, such as the pygmy mammoth shown in [\[link\]](#), can be calculated with accuracy if it is not much older than about 50,000 years. Other elements have isotopes with different half lives. For example, ^{40}K (potassium-40) has a half-life of 1.25 billion years, and ^{235}U (Uranium 235) has a half-life of about 700 million years. Through the use of radiometric dating, scientists can study the age of fossils or other remains of extinct organisms to understand how organisms have evolved from earlier species. The age of carbon-containing remains less than about 50,000 years old, such as this pygmy

mammoth, can be determined using carbon dating.
(credit: Bill Faulkner, NPS)



Link to Learning



To learn more about atoms, isotopes, and how to tell one isotope from another, run the simulation.

https://openstax.org/l/atoms_isotopes

The periodic table shows the atomic mass and atomic number of each element. The atomic number appears above the symbol for the element and the approximate atomic mass appears below it.

The Periodic Table

The different elements are organized and displayed in the **periodic table**. Devised by Russian chemist Dmitri Mendeleev (1834–1907) in 1869, the table groups elements that, although unique, share certain chemical properties with other elements. The properties of elements are responsible for their physical state at room temperature: they may be gases, solids, or liquids. Elements also have specific **chemical reactivity**, the ability to combine and to chemically bond with each other.

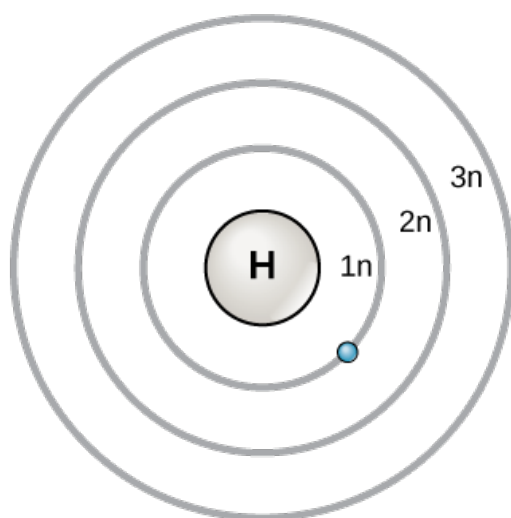
In the periodic table, shown in [\[link\]](#), the elements are organized and displayed according to their atomic number and are arranged in a series of rows and columns based on shared chemical and physical properties. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear, as well as its atomic number of six (in the upper left-hand corner) and its atomic mass of 12.11.

bump it up to a higher energy shell, but this situation is unstable, and the electron quickly decays back to the ground state. In the process, a photon of light is released.

Electron Shells and the Bohr Model

It should be stressed that there is a connection between the number of protons in an element, the atomic number that distinguishes one element from another, and the number of electrons it has. In all electrically neutral atoms, the number of electrons is the same as the number of protons. Thus, each element, at least when electrically neutral, has a characteristic number of electrons equal to its atomic number.

An early model of the atom was developed in 1913 by Danish scientist Niels Bohr (1885–1962). The Bohr model shows the atom as a central nucleus containing protons and neutrons, with the electrons in circular **orbitals** at specific distances from the nucleus, as illustrated in [\[link\]](#). These orbits form electron shells or energy levels, which are a way of visualizing the number of electrons in the outermost shells. These energy levels are designated by a number and the symbol “n.” For example, 1n represents the first energy level located closest to the nucleus.





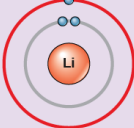
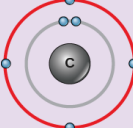
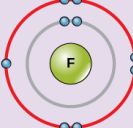
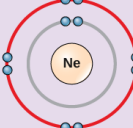

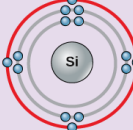
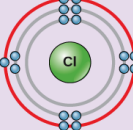
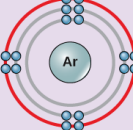
Electrons fill orbitals in a consistent order: they first fill the orbitals closest to the nucleus, then they continue to fill orbitals of increasing energy further from the nucleus. If there are multiple orbitals of equal energy, they will be filled with one electron in each energy level before a second electron is added. The electrons of the outermost energy level determine the energetic stability of the atom and its tendency to form chemical bonds with other atoms to form molecules.

Under standard conditions, atoms fill the inner shells first, often resulting in a variable number of electrons in the outermost shell. The innermost shell has a maximum of two electrons but the next two

electron shells can each have a maximum of eight electrons. This is known as the **octet rule**, which states, with the exception of the innermost shell, that atoms are more stable energetically when they have eight electrons in their **valence shell**, the outermost electron shell. Examples of some neutral atoms and their electron configurations are shown in [\[link\]](#). Notice that in this [\[link\]](#), helium has a complete outer electron shell, with two electrons filling its first and only shell. Similarly, neon has a complete outer $2n$ shell containing eight electrons. In contrast, chlorine and sodium have seven and one in their outer shells, respectively, but theoretically they would be more energetically stable if they followed the octet rule and had eight.

Art Connection

Bohr diagrams indicate how many electrons fill each principal shell. Group 18 elements (helium, neon, and argon are shown) have a full outer, or valence, shell. A full valence shell is the most stable electron configuration. Elements in other groups have partially filled valence shells and gain or lose electrons to achieve a stable electron configuration.

	Group 1	Group 14	Group 17	Group 18
Period 1 (1n is filling)				
Period 2 (2n is filling)				
Period 3 (3n is filling)				

An atom may give, take, or share electrons with another atom to achieve a full valence shell, the most stable electron configuration. Looking at this figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration? How many electrons do elements in groups 14 and 17 need to gain to achieve a stable configuration?

Understanding that the organization of the periodic table is based on the total number of protons (and electrons) helps us know how electrons are distributed among the outer shell. The periodic table is arranged in columns and rows based on the number of electrons and where these electrons are located. Take a closer look at the some of the elements in the table's far right column in [\[link\]](#). The group 18 atoms helium (He), neon (Ne), and

argon (Ar) all have filled outer electron shells, making it unnecessary for them to share electrons with other atoms to attain stability; they are highly stable as single atoms. Their non-reactivity has resulted in their being named the **inert gases** (or **noble gases**). Compare this to the group 1 elements in the left-hand column. These elements, including hydrogen (H), lithium (Li), and sodium (Na), all have one electron in their outermost shells. That means that they can achieve a stable configuration and a filled outer shell by donating or sharing one electron with another atom or a molecule such as water. Hydrogen will donate or share its electron to achieve this configuration, while lithium and sodium will donate their electron to become stable. As a result of losing a negatively charged electron, they become positively charged **ions**. Group 17 elements, including fluorine and chlorine, have seven electrons in their outmost shells, so they tend to fill this shell with an electron from other atoms or molecules, making them negatively charged ions. Group 14 elements, of which carbon is the most important to living systems, have four electrons in their outer shell allowing them to make several covalent bonds (discussed below) with other atoms. Thus, the columns of the periodic table represent the potential shared state of these elements' outer electron shells that is responsible for their similar chemical characteristics.

The *s* subshells are shaped like spheres. Both the $1n$ and $2n$ principal shells have an *s* orbital, but the size

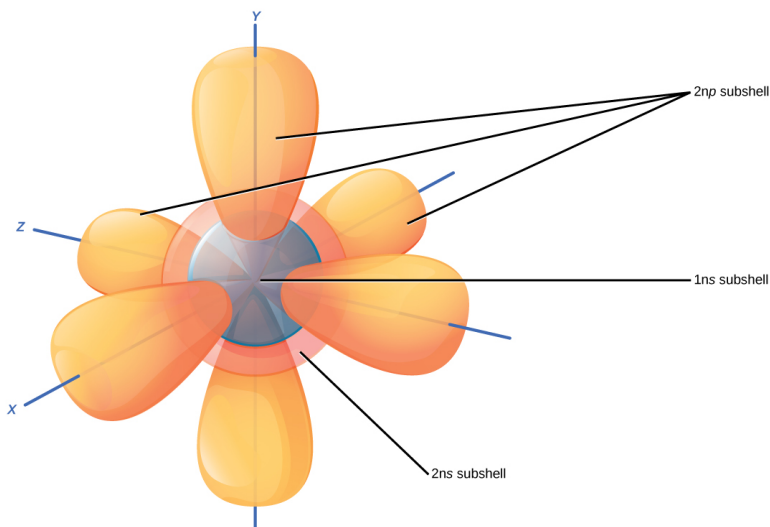
of the sphere is larger in the $2n$ orbital. Each sphere is a single orbital. p subshells are made up of three dumbbell-shaped orbitals. Principal shell $2n$ has a p subshell, but shell 1 does not.

Electron Orbitals

Although useful to explain the reactivity and chemical bonding of certain elements, the Bohr model of the atom does not accurately reflect how electrons are spatially distributed surrounding the nucleus. They do not circle the nucleus like the earth orbits the sun, but are found in **electron orbitals**. These relatively complex shapes result from the fact that electrons behave not just like particles, but also like waves. Mathematical equations from quantum mechanics known as wave functions can predict within a certain level of probability where an electron might be at any given time. The area where an electron is most likely to be found is called its orbital.

Recall that the Bohr model depicts an atom's electron shell configuration. Within each electron shell are subshells, and each subshell has a specified number of orbitals containing electrons. While it is impossible to calculate exactly where an electron is located, scientists know that it is most probably located within its orbital path. Subshells are designated by the letter s , p , d , and f . The s subshell is spherical in shape and has one orbital. Principal

shell $1n$ has only a single s orbital, which can hold two electrons. Principal shell $2n$ has one s and one p subshell, and can hold a total of eight electrons. The p subshell has three dumbbell-shaped orbitals, as illustrated in [\[link\]](#). Subshells d and f have more complex shapes and contain five and seven orbitals, respectively. These are not shown in the illustration. Principal shell $3n$ has s , p , and d subshells and can hold 18 electrons. Principal shell $4n$ has s , p , d and f orbitals and can hold 32 electrons. Moving away from the nucleus, the number of electrons and orbitals found in the energy levels increases. Progressing from one atom to the next in the periodic table, the electron structure can be worked out by fitting an extra electron into the next available orbital.



The closest orbital to the nucleus, called the $1s$ orbital, can hold up to two electrons. This orbital is equivalent to the innermost electron shell of the

Bohr model of the atom. It is called the $1s$ orbital because it is spherical around the nucleus. The $1s$ orbital is the closest orbital to the nucleus, and it is always filled first, before any other orbital can be filled. Hydrogen has one electron; therefore, it has only one spot within the $1s$ orbital occupied. This is designated as $1s_1$, where the superscripted 1 refers to the one electron within the $1s$ orbital. Helium has two electrons; therefore, it can completely fill the $1s$ orbital with its two electrons. This is designated as $1s_2$, referring to the two electrons of helium in the $1s$ orbital. On the periodic table [\[link\]](#), hydrogen and helium are the only two elements in the first row (period); this is because they only have electrons in their first shell, the $1s$ orbital. Hydrogen and helium are the only two elements that have the $1s$ and no other electron orbitals in the electrically neutral state.

The second electron shell may contain eight electrons. This shell contains another spherical s orbital and three “dumbbell” shaped p orbitals, each of which can hold two electrons, as shown in [\[link\]](#). After the $1s$ orbital is filled, the second electron shell is filled, first filling its $2s$ orbital and then its three p orbitals. When filling the p orbitals, each takes a single electron; once each p orbital has an electron, a second may be added. Lithium (Li) contains three electrons that occupy the first and second shells. Two electrons fill the $1s$ orbital, and the third electron then fills the $2s$ orbital. Its

electron configuration is $1s^2 2s^1$. Neon (Ne), on the other hand, has a total of ten electrons: two are in its innermost $1s$ orbital and eight fill its second shell (two each in the $2s$ and three p orbitals); thus, it is an inert gas and energetically stable as a single atom that will rarely form a chemical bond with other atoms. Larger elements have additional orbitals, making up the third electron shell. While the concepts of electron shells and orbitals are closely related, orbitals provide a more accurate depiction of the electron configuration of an atom because the orbital model specifies the different shapes and special orientations of all the places that electrons may occupy.

Link to Learning



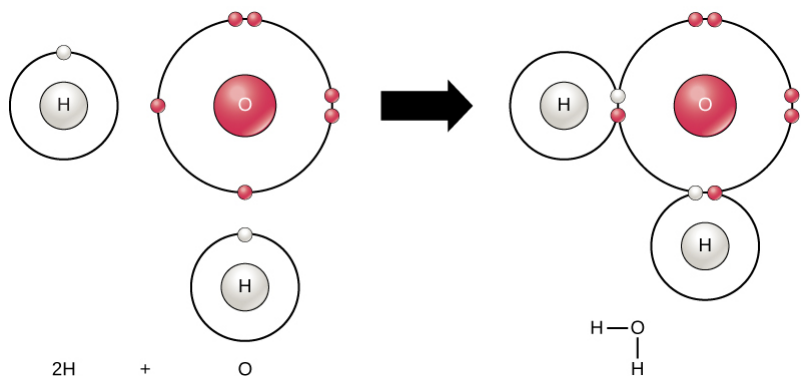
Watch this visual animation to see the spatial arrangement of the p and s orbitals.

<https://www.openstaxcollege.org/1/orbitals>

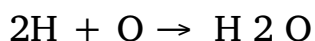
Two or more atoms may bond with each other to form a molecule. When two hydrogens and an oxygen share electrons via covalent bonds, a water molecule is formed. The oxygen atoms in an O_2 molecule are joined by a double bond.

Chemical Reactions and Molecules

All elements are most stable when their outermost shell is filled with electrons according to the octet rule. This is because it is energetically favorable for atoms to be in that configuration and it makes them stable. However, since not all elements have enough electrons to fill their outermost shells, atoms form **chemical bonds** with other atoms thereby obtaining the electrons they need to attain a stable electron configuration. When two or more atoms chemically bond with each other, the resultant chemical structure is a molecule. The familiar water molecule, H_2O , consists of two hydrogen atoms and one oxygen atom; these bond together to form water, as illustrated in [\[link\]](#). Atoms can form molecules by donating, accepting, or sharing electrons to fill their outer shells.

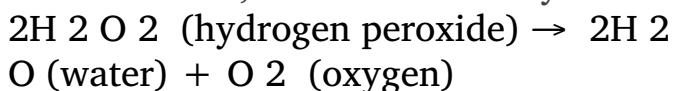


Chemical reactions occur when two or more atoms bond together to form molecules or when bonded atoms are broken apart. The substances used in the beginning of a chemical reaction are called the **reactants** (usually found on the left side of a chemical equation), and the substances found at the end of the reaction are known as the **products** (usually found on the right side of a chemical equation). An arrow is typically drawn between the reactants and products to indicate the direction of the chemical reaction; this direction is not always a “one-way street.” For the creation of the water molecule shown above, the chemical equation would be:

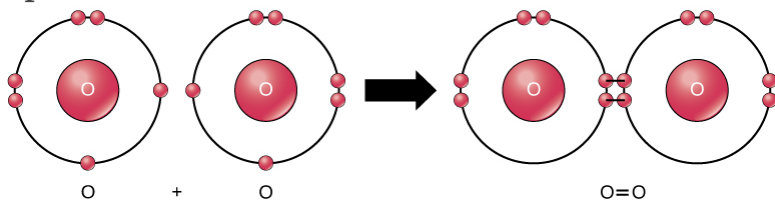


An example of a simple chemical reaction is the breaking down of hydrogen peroxide molecules, each of which consists of two hydrogen atoms bonded to two oxygen atoms (H_2O_2). The reactant hydrogen peroxide is broken down into water, containing one oxygen atom bound to two hydrogen

atoms (H₂O), and oxygen, which consists of two bonded oxygen atoms (O₂). In the equation below, the reaction includes two hydrogen peroxide molecules and two water molecules. This is an example of a **balanced chemical equation**, wherein the number of atoms of each element is the same on each side of the equation. According to the law of conservation of matter, the number of atoms before and after a chemical reaction should be equal, such that no atoms are, under normal circumstances, created or destroyed.



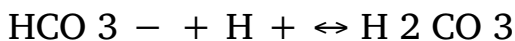
Even though all of the reactants and products of this reaction are molecules (each atom remains bonded to at least one other atom), in this reaction only hydrogen peroxide and water are representatives of **compounds**: they contain atoms of more than one type of element. Molecular oxygen, on the other hand, as shown in [\[link\]](#), consists of two doubly bonded oxygen atoms and is not classified as a compound but as a homonuclear molecule.



Some chemical reactions, such as the one shown above, can proceed in one direction until the reactants are all used up. The equations that

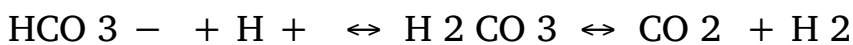
describe these reactions contain a unidirectional arrow and are **irreversible**. **Reversible reactions** are those that can go in either direction. In reversible reactions, reactants are turned into products, but when the concentration of product goes beyond a certain threshold (characteristic of the particular reaction), some of these products will be converted back into reactants; at this point, the designations of products and reactants are reversed. This back and forth continues until a certain relative balance between reactants and products occurs—a state called **equilibrium**. These situations of reversible reactions are often denoted by a chemical equation with a double headed arrow pointing towards both the reactants and products.

For example, in human blood, excess hydrogen ions (H^+) bind to bicarbonate ions (HCO_3^-) forming an equilibrium state with carbonic acid (H_2CO_3). If carbonic acid were added to this system, some of it would be converted to bicarbonate and hydrogen ions.



In biological reactions, however, equilibrium is rarely obtained because the concentrations of the reactants or products or both are constantly changing, often with a product of one reaction being a reactant for another. To return to the example of excess hydrogen ions in the blood, the formation of carbonic acid will be the major direction of the

reaction. However, the carbonic acid can also leave the body as carbon dioxide gas (via exhalation) instead of being converted back to bicarbonate ion, thus driving the reaction to the right by the chemical law known as **law of mass action**. These reactions are important for maintaining the homeostasis of our blood.



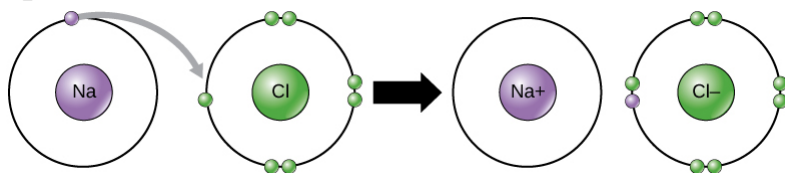
In the formation of an ionic compound, metals lose electrons and nonmetals gain electrons to achieve an octet.

Ions and Ionic Bonds

Some atoms are more stable when they gain or lose an electron (or possibly two) and form ions. This fills their outermost electron shell and makes them energetically more stable. Because the number of electrons does not equal the number of protons, each ion has a net charge. **Cations** are positive ions that are formed by losing electrons. Negative ions are formed by gaining electrons and are called anions. **Anions** are designated by their elemental name being altered to end in “-ide”: the anion of chlorine is called chloride, and the anion of sulfur is called sulfide, for example.

This movement of electrons from one element to another is referred to as **electron transfer**. As [\[link\]](#) illustrates, sodium (Na) only has one electron in its outer electron shell. It takes less energy for sodium

to donate that one electron than it does to accept seven more electrons to fill the outer shell. If sodium loses an electron, it now has 11 protons, 11 neutrons, and only 10 electrons, leaving it with an overall charge of $+1$. It is now referred to as a sodium ion. Chlorine (Cl) in its lowest energy state (called the ground state) has seven electrons in its outer shell. Again, it is more energy-efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons, 17 neutrons, and 18 electrons, giving it a net negative (-1) charge. It is now referred to as a chloride ion. In this example, sodium will donate its one electron to empty its shell, and chlorine will accept that electron to fill its shell. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a $+1$ (sodium cation) or -1 (chloride anion) charge. Note that these transactions can normally only take place simultaneously: in order for a sodium atom to lose an electron, it must be in the presence of a suitable recipient like a chlorine atom.



Ionic bonds are formed between ions with opposite charges. For instance, positively charged sodium

ions and negatively charged chloride ions bond together to make crystals of sodium chloride, or table salt, creating a crystalline molecule with zero net charge.

Certain salts are referred to in physiology as **electrolytes** (including sodium, potassium, and calcium), ions necessary for nerve impulse conduction, muscle contractions and water balance. Many sports drinks and dietary supplements provide these ions to replace those lost from the body via sweating during exercise.

Whether a molecule is polar or nonpolar depends both on bond type and molecular shape. Both water and carbon dioxide have polar covalent bonds, but carbon dioxide is linear, so the partial charges on the molecule cancel each other out.

Covalent Bonds and Other Bonds and Interactions

Another way the octet rule can be satisfied is by the sharing of electrons between atoms to form **covalent bonds**. These bonds are stronger and much more common than ionic bonds in the molecules of living organisms. Covalent bonds are commonly found in carbon-based organic molecules, such as our DNA and proteins. Covalent bonds are also found in inorganic molecules like H_2O , CO_2 , and O_2 . One, two, or three pairs of electrons may be shared, making single, double, and triple bonds,

respectively. The more covalent bonds between two atoms, the stronger their connection. Thus, triple bonds are the strongest.

The strength of different levels of covalent bonding is one of the main reasons living organisms have a difficult time in acquiring nitrogen for use in constructing their molecules, even though molecular nitrogen, N_2 , is the most abundant gas in the atmosphere. Molecular nitrogen consists of two nitrogen atoms triple bonded to each other and, as with all molecules, the sharing of these three pairs of electrons between the two nitrogen atoms allows for the filling of their outer electron shells, making the molecule more stable than the individual nitrogen atoms. This strong triple bond makes it difficult for living systems to break apart this nitrogen in order to use it as constituents of proteins and DNA.

The formation of water molecules provides an example of covalent bonding. The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds, as shown in [\[link\]](#). The electron from the hydrogen splits its time between the incomplete outer shell of the hydrogen atoms and the incomplete outer shell of the oxygen atoms. To completely fill the outer shell of oxygen, which has six electrons in its outer shell but which would be more stable with eight, two electrons (one from each hydrogen atom) are

needed: hence the well-known formula H_2O . The electrons are shared between the two elements to fill the outer shell of each, making both elements more stable.

Link to Learning



View this short video to see an animation of ionic and covalent bonding.

https://www.openstaxcollege.org/l/ionic_covalent

Polar Covalent Bonds

There are two types of covalent bonds: polar and nonpolar. In a **polar covalent bond**, shown in [\[link\]](#), the electrons are unequally shared by the atoms and are attracted more to one nucleus than the other. Because of the unequal distribution of electrons between the atoms of different elements, a slightly positive ($\delta+$) or slightly negative ($\delta-$)

charge develops. This partial charge is an important property of water and accounts for many of its characteristics.

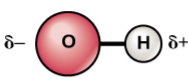
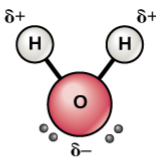
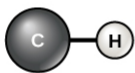
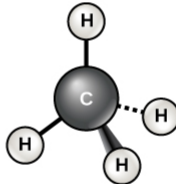
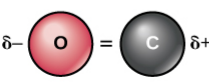
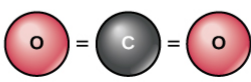
Water is a polar molecule, with the hydrogen atoms acquiring a partial positive charge and the oxygen a partial negative charge. This occurs because the nucleus of the oxygen atom is more attractive to the electrons of the hydrogen atoms than the hydrogen nucleus is to the oxygen's electrons. Thus oxygen has a higher **electronegativity** than hydrogen and the shared electrons spend more time in the vicinity of the oxygen nucleus than they do near the nucleus of the hydrogen atoms, giving the atoms of oxygen and hydrogen slightly negative and positive charges, respectively. Another way of stating this is that the probability of finding a shared electron near an oxygen nucleus is more likely than finding it near a hydrogen nucleus. Either way, the atom's relative electronegativity contributes to the development of partial charges whenever one element is significantly more electronegative than the other, and the charges generated by these polar bonds may then be used for the formation of hydrogen bonds based on the attraction of opposite partial charges. (Hydrogen bonds, which are discussed in detail below, are weak bonds between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules.) Since macromolecules often have atoms within them that differ in electronegativity, polar bonds are often

present in organic molecules.

Nonpolar Covalent Bonds

Nonpolar covalent bonds form between two atoms of the same element or between different elements that share electrons equally. For example, molecular oxygen (O_2) is nonpolar because the electrons will be equally distributed between the two oxygen atoms.

Another example of a nonpolar covalent bond is methane (CH_4), also shown in [\[link\]](#). Carbon has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one, making a stable outer shell of eight electrons. Carbon and hydrogen do not have the same electronegativity but are similar; thus, nonpolar bonds form. The hydrogen atoms each need one electron for their outermost shell, which is filled when it contains two electrons. These elements share the electrons equally among the carbons and the hydrogen atoms, creating a nonpolar covalent molecule.

	Bond type	Molecular shape	Molecular type
Water	 Polar covalent	 Bent	Polar
Methane	 Nonpolar covalent	 Tetrahedral	Nonpolar
Carbon dioxide	 Polar covalent	 Linear	Nonpolar

Hydrogen Bonds and Van Der Waals Interactions

Ionic and covalent bonds between elements require energy to break. Ionic bonds are not as strong as covalent, which determines their behavior in biological systems. However, not all bonds are ionic or covalent bonds. Weaker bonds can also form between molecules. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions. Without these two types of bonds, life as we know it would not exist. Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells.

When polar covalent bonds containing hydrogen form, the hydrogen in that bond has a slightly positive charge because hydrogen's electron is pulled more strongly toward the other element and away from the hydrogen. Because the hydrogen is slightly positive, it will be attracted to neighboring negative charges. When this happens, a weak interaction occurs between the $\delta+$ of the hydrogen from one molecule and the $\delta-$ charge on the more electronegative atoms of another molecule, usually oxygen or nitrogen, or within the same molecule. This interaction is called a **hydrogen bond**. This type of bond is common and occurs regularly between water molecules. Individual hydrogen bonds are weak and easily broken; however, they occur in very large numbers in water and in organic polymers, creating a major force in combination. Hydrogen bonds are also responsible for zipping together the DNA double helix.

Like hydrogen bonds, **van der Waals interactions** are weak attractions or interactions between molecules. Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities, which are not always symmetrical around an atom. For these attractions to happen, the molecules need to be very close to one another. These bonds—along with ionic, covalent, and hydrogen bonds—contribute to the three-dimensional structure of the proteins in our cells

that is necessary for their proper function.

Career Connection

Pharmaceutical Chemist

Pharmaceutical chemists are responsible for the development of new drugs and trying to determine the mode of action of both old and new drugs.

They are involved in every step of the drug development process. Drugs can be found in the natural environment or can be synthesized in the laboratory. In many cases, potential drugs found in nature are changed chemically in the laboratory to make them safer and more effective, and sometimes synthetic versions of drugs substitute for the version found in nature.

After the initial discovery or synthesis of a drug, the chemist then develops the drug, perhaps chemically altering it, testing it to see if the drug is toxic, and then designing methods for efficient large-scale production. Then, the process of getting the drug approved for human use begins. In the United States, drug approval is handled by the Food and Drug Administration (FDA) and involves a series of large-scale experiments using human subjects to make sure the drug is not harmful and effectively treats the condition it aims to treat. This process often takes several years and requires the participation of physicians and scientists, in addition to chemists, to complete testing and gain

approval.

An example of a drug that was originally discovered in a living organism is Paclitaxel (Taxol), an anti-cancer drug used to treat breast cancer. This drug was discovered in the bark of the pacific yew tree. Another example is aspirin, originally isolated from willow tree bark. Finding drugs often means testing hundreds of samples of plants, fungi, and other forms of life to see if any biologically active compounds are found within them. Sometimes, traditional medicine can give modern medicine clues to where an active compound can be found. For example, the use of willow bark to make medicine has been known for thousands of years, dating back to ancient Egypt. It was not until the late 1800s, however, that the aspirin molecule, known as acetylsalicylic acid, was purified and marketed for human use.

Occasionally, drugs developed for one use are found to have unforeseen effects that allow these drugs to be used in other, unrelated ways. For example, the drug minoxidil (Rogaine) was originally developed to treat high blood pressure. When tested on humans, it was noticed that individuals taking the drug would grow new hair. Eventually the drug was marketed to men and women with baldness to restore lost hair.

The career of the pharmaceutical chemist may involve detective work, experimentation, and drug development, all with the goal of making human beings healthier.

Section Summary

Matter is anything that occupies space and has mass. It is made up of elements. All of the 92 elements that occur naturally have unique qualities that allow them to combine in various ways to create molecules, which in turn combine to form cells, tissues, organ systems, and organisms. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can be transferred, shared, or cause charge disparities between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

Art Connections

[\[link\]](#) How many neutrons do carbon-12 and carbon-13 have, respectively?

[\[link\]](#) Carbon-12 has six neutrons. Carbon-13 has seven neutrons.

[\[link\]](#) An atom may give, take, or share electrons with another atom to achieve a full valence shell, the most stable electron configuration. Looking at this figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration? How many electrons do elements in groups 14 and 17 need to gain to achieve a stable configuration?

[\[link\]](#) Elements in group 1 need to lose one electron to achieve a stable electron configuration. Elements in groups 14 and 17 need to gain four and one electrons, respectively, to achieve a stable configuration.

Review Questions

If xenon has an atomic number of 54 and a mass number of 108, how many neutrons does it have?

1. 54
 2. 27
 3. 100
 4. 108
-

A

Atoms that vary in the number of neutrons found in their nuclei are called ____.

1. ions
2. neutrons
3. neutral atoms
4. isotopes

D

Potassium has an atomic number of 19. What is its electron configuration?

1. shells 1 and 2 are full, and shell 3 has nine electrons
2. shells 1, 2 and 3 are full and shell 4 has three electrons
3. shells 1, 2 and 3 are full and shell 4 has one electron
4. shells 1, 2 and 3 are full and no other electrons are present

C

Which type of bond represents a weak chemical

bond?

1. hydrogen bond
2. atomic bond
3. covalent bond
4. nonpolar covalent bond

A

Free Response

What makes ionic bonds different from covalent bonds?

Ionic bonds are created between ions. The electrons are not shared between the atoms, but rather are associated more with one ion than the other. Ionic bonds are strong bonds, but are weaker than covalent bonds, meaning it takes less energy to break an ionic bond compared with a covalent one.

Why are hydrogen bonds and van der Waals interactions necessary for cells?

Hydrogen bonds and van der Waals interactions form weak associations between different molecules or within different regions of the same molecule. They provide the structure and shape necessary for proteins and DNA within cells so that they function properly.

Glossary

anion

negative ion that is formed by an atom gaining one or more electrons

atom

the smallest unit of matter that retains all of the chemical properties of an element

atomic mass

calculated mean of the mass number for an element's isotopes

atomic number

total number of protons in an atom

balanced chemical equation

statement of a chemical reaction with the number of each type of atom equalized for both the products and reactants

cation

positive ion that is formed by an atom losing

one or more electrons

chemical bond

interaction between two or more of the same or different atoms that results in the formation of molecules

chemical reaction

process leading to the rearrangement of atoms in molecules

chemical reactivity

the ability to combine and to chemically bond with each other

compound

substance composed of molecules consisting of atoms of at least two different elements

covalent bond

type of strong bond formed between two of the same or different elements; forms when electrons are shared between atoms

electrolyte

ion necessary for nerve impulse conduction, muscle contractions and water balance

electron

negatively charged subatomic particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a

negative charge of -1 unit

electron configuration

arrangement of electrons in an atom's
electron shell (for example, $1s^2 2s^2 2p^6$)

electron orbital

how electrons are spatially distributed
surrounding the nucleus; the area where an
electron is most likely to be found

electron transfer

movement of electrons from one element to
another; important in creation of ionic bonds

electronegativity

ability of some elements to attract electrons
(often of hydrogen atoms), acquiring partial
negative charges in molecules and creating
partial positive charges on the hydrogen
atoms

element

one of 118 unique substances that cannot be
broken down into smaller substances; each
element has unique properties and a specified
number of protons

equilibrium

steady state of relative reactant and product
concentration in reversible chemical reactions
in a closed system

hydrogen bond

weak bond between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules

inert gas

(also, noble gas) element with filled outer electron shell that is unreactive with other atoms

ion

atom or chemical group that does not contain equal numbers of protons and electrons

ionic bond

chemical bond that forms between ions with opposite charges (cations and anions)

irreversible chemical reaction

chemical reaction where reactants proceed uni-directionally to form products

isotope

one or more forms of an element that have different numbers of neutrons

law of mass action

chemical law stating that the rate of a reaction is proportional to the concentration of the reacting substances

mass number

total number of protons and neutrons in an atom

matter

anything that has mass and occupies space

molecule

two or more atoms chemically bonded together

neutron

uncharged particle that resides in the nucleus of an atom; has a mass of one amu

noble gas

see inert gas

nonpolar covalent bond

type of covalent bond that forms between atoms when electrons are shared equally between them

nucleus

core of an atom; contains protons and neutrons

octet rule

rule that atoms are most stable when they hold eight electrons in their outermost shells

orbital

region surrounding the nucleus; contains electrons

periodic table

organizational chart of elements indicating the atomic number and atomic mass of each element; provides key information about the properties of the elements

polar covalent bond

type of covalent bond that forms as a result of unequal sharing of electrons, resulting in the creation of slightly positive and slightly negative charged regions of the molecule

product

molecule found on the right side of a chemical equation

proton

positively charged particle that resides in the nucleus of an atom; has a mass of one amu and a charge of $+1$

radioisotope

isotope that emits radiation composed of subatomic particles to form more stable elements

reactant

molecule found on the left side of a chemical equation

reversible chemical reaction

chemical reaction that functions bi-

directionally, where products may turn into reactants if their concentration is great enough

valence shell

outermost shell of an atom

van der Waals interaction

very weak interaction between molecules due to temporary charges attracting atoms that are very close together

Carbon

By the end of this section, you will be able to:

- Explain why carbon is important for life
- Describe the role of functional groups in biological molecules

Cells are made of many complex molecules called macromolecules, such as proteins, nucleic acids (RNA and DNA), carbohydrates, and lipids. The macromolecules are a subset of **organic molecules** (any carbon-containing liquid, solid, or gas) that are especially important for life. The fundamental component for all of these macromolecules is carbon. The carbon atom has unique properties that allow it to form covalent bonds to as many as four different atoms, making this versatile element ideal to serve as the basic structural component, or “backbone,” of the macromolecules.

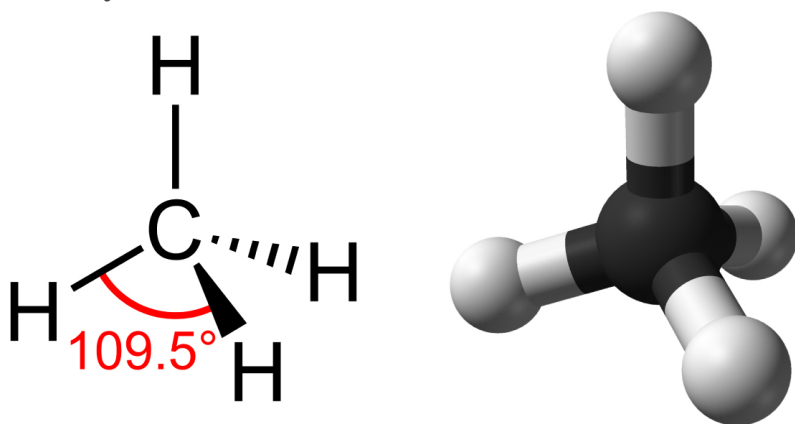
Individual carbon atoms have an incomplete outermost electron shell. With an atomic number of 6 (six electrons and six protons), the first two electrons fill the inner shell, leaving four in the second shell. Therefore, carbon atoms can form up to four covalent bonds with other atoms to satisfy the octet rule. The methane molecule provides an example: it has the chemical formula CH_4 . Each of its four hydrogen atoms forms a single covalent bond with the carbon atom by sharing a pair of electrons. This results in a filled outermost shell.

Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart. When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those found in ethane, are able to rotate. Double bonds, like those found in ethene cannot rotate, so the atoms on either side are locked in place. Carbon can form five- and six-membered rings. Single or double bonds may connect the carbons in the ring, and nitrogen may be substituted for carbon.

Hydrocarbons

Hydrocarbons are organic molecules consisting entirely of carbon and hydrogen, such as methane (CH_4) described above. We often use hydrocarbons in our daily lives as fuels—like the propane in a gas grill or the butane in a lighter. The many covalent bonds between the atoms in hydrocarbons store a great amount of energy, which is released when these molecules are burned (oxidized). Methane, an excellent fuel, is the simplest hydrocarbon molecule, with a central carbon atom bonded to four different hydrogen atoms, as illustrated in [\[link\]](#). The geometry of the methane molecule, where the atoms reside in three dimensions, is determined by the shape of its electron orbitals. The carbons and the four hydrogen atoms form a shape known as a tetrahedron, with four triangular faces; for this

reason, methane is described as having tetrahedral geometry.

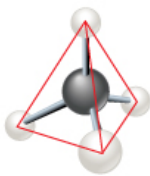
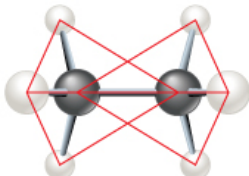
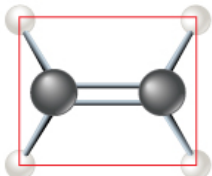


As the backbone of the large molecules of living things, hydrocarbons may exist as linear carbon chains, carbon rings, or combinations of both. Furthermore, individual carbon-to-carbon bonds may be single, double, or triple covalent bonds, and each type of bond affects the geometry of the molecule in a specific way. This three-dimensional shape or conformation of the large molecules of life (macromolecules) is critical to how they function.

Hydrocarbon Chains

Hydrocarbon chains are formed by successive bonds between carbon atoms and may be branched or unbranched. Furthermore, the overall geometry of the molecule is altered by the different geometries of single, double, and triple covalent bonds, illustrated in [\[link\]](#). The hydrocarbons ethane,

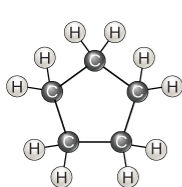
ethene, and ethyne serve as examples of how different carbon-to-carbon bonds affect the geometry of the molecule. The names of all three molecules start with the prefix “eth-,” which is the prefix for two carbon hydrocarbons. The suffixes “-ane,” “-ene,” and “-yne” refer to the presence of single, double, or triple carbon-carbon bonds, respectively. Thus, propane, propene, and propyne follow the same pattern with three carbon molecules, butane, butene, and butyne for four carbon molecules, and so on. Double and triple bonds change the geometry of the molecule: single bonds allow rotation along the axis of the bond, whereas double bonds lead to a planar configuration and triple bonds to a linear one. These geometries have a significant impact on the shape a particular molecule can assume.

Methane (CH ₄)	Ethane (C ₂ H ₆)	Ethene (C ₂ H ₄)
		
Tetrahedral (single bond)	Tetrahedral (single bond)	Planar (double bond)

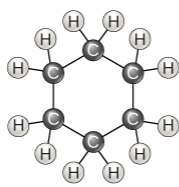
Hydrocarbon Rings

So far, the hydrocarbons we have discussed have been **aliphatic hydrocarbons**, which consist of linear chains of carbon atoms. Another type of hydrocarbon, **aromatic hydrocarbons**, consists of

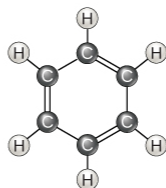
closed rings of carbon atoms. Ring structures are found in hydrocarbons, sometimes with the presence of double bonds, which can be seen by comparing the structure of cyclohexane to benzene in [\[link\]](#). Examples of biological molecules that incorporate the benzene ring include some amino acids and cholesterol and its derivatives, including the hormones estrogen and testosterone. The benzene ring is also found in the herbicide 2,4-D. Benzene is a natural component of crude oil and has been classified as a carcinogen. Some hydrocarbons have both aliphatic and aromatic portions; beta-carotene is an example of such a hydrocarbon.



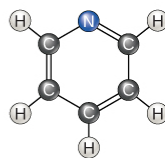
Cyclopentane



Cyclohexane



Benzene



Pyridine

These space-filling models show a *cis* (oleic acid) and a *trans* (eliadic acid) fatty acid. Notice the bend in the molecule cause by the *cis* configuration.

Isomers

The three-dimensional placement of atoms and chemical bonds within organic molecules is central to understanding their chemistry. Molecules that share the same chemical formula but differ in the placement (structure) of their atoms and/or chemical bonds are known as **isomers**. **Structural isomers** (like butane and isobutene shown in [\[link\]](#))

a) differ in the placement of their covalent bonds: both molecules have four carbons and ten hydrogens (C_4H_{10}), but the different arrangement of the atoms within the molecules leads to differences in their chemical properties. For example, due to their different chemical properties, butane is suited for use as a fuel for cigarette lighters and torches, whereas isobutene is suited for use as a refrigerant and a propellant in spray cans.

Geometric isomers, on the other hand, have similar placements of their covalent bonds but differ in how these bonds are made to the surrounding atoms, especially in carbon-to-carbon double bonds. In the simple molecule butene (C_4H_8), the two methyl groups (CH_3) can be on either side of the double covalent bond central to the molecule, as illustrated in [\[link\]](#) b. When the carbons are bound on the same side of the double bond, this is the *cis* configuration; if they are on opposite sides of the double bond, it is a *trans* configuration. In the *trans* configuration, the carbons form a more or less linear structure, whereas the carbons in the *cis* configuration make a bend (change in direction) of the carbon backbone.

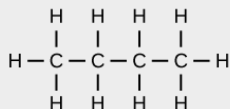
Art Connection

Molecules that have the same number and type of atoms arranged differently are called isomers. (a)

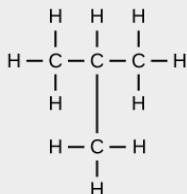
Structural isomers have a different covalent arrangement of atoms. (b) Geometric isomers have a different arrangement of atoms around a double bond. (c) Enantiomers are mirror images of each other.

(a) Structural isomers

Butane

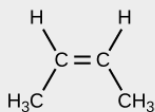


Isobutane



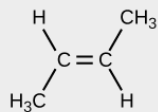
(b) Geometric isomers

cis-2-butene



methyl groups on same side of double bond

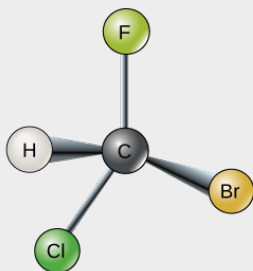
trans-2-butene



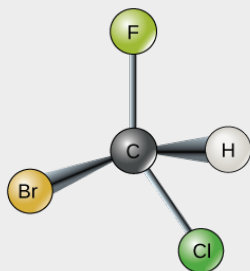
methyl groups on opposite sides of double bond

(c) Enantiomers

L-isomer



D-isomer



Which of the following statements is false?

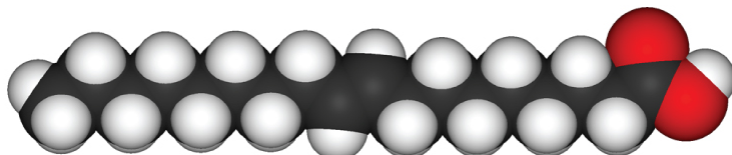
1. Molecules with the formulas $\text{CH}_3\text{CH}_2\text{COOH}$

and $C_3H_6O_2$ could be structural isomers.

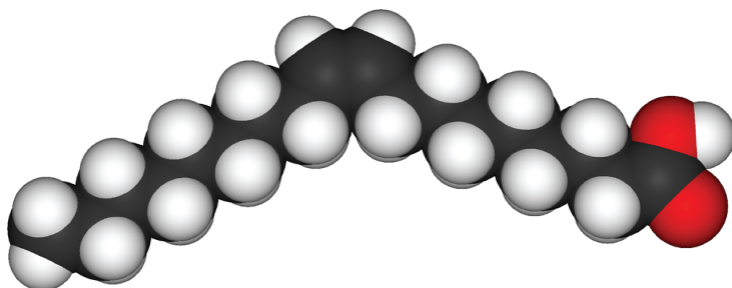
2. Molecules must have a double bond to be *cis-trans* isomers.
3. To be enantiomers, a molecule must have at least three different atoms or groups connected to a central carbon.
4. To be enantiomers, a molecule must have at least four different atoms or groups connected to a central carbon.

In triglycerides (fats and oils), long carbon chains known as fatty acids may contain double bonds, which can be in either the *cis* or *trans* configuration, illustrated in [\[link\]](#). Fats with at least one double bond between carbon atoms are unsaturated fats. When some of these bonds are in the *cis* configuration, the resulting bend in the carbon backbone of the chain means that triglyceride molecules cannot pack tightly, so they remain liquid (oil) at room temperature. On the other hand, triglycerides with *trans* double bonds (popularly called trans fats), have relatively linear fatty acids that are able to pack tightly together at room temperature and form solid fats. In the human diet, trans fats are linked to an increased risk of cardiovascular disease, so many food manufacturers have reduced or eliminated their use in recent years. In contrast to unsaturated fats, triglycerides without double bonds between carbon atoms are called

saturated fats, meaning that they contain all the hydrogen atoms available. Saturated fats are a solid at room temperature and usually of animal origin.



Elaidic acid



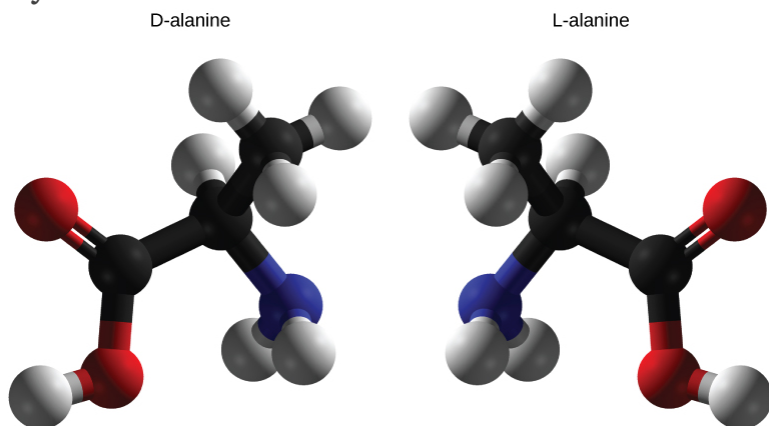
Oleic acid

D-alanine and L-alanine are examples of enantiomers or mirror images. Only the L-forms of amino acids are used to make proteins.

Enantiomers

Enantiomers are molecules that share the same chemical structure and chemical bonds but differ in the three-dimensional placement of atoms so that they are mirror images. As shown in [\[link\]](#), an amino acid alanine example, the two structures are non-superimposable. In nature, only the L-forms of amino acids are used to make proteins. Some D forms of amino acids are seen in the cell walls of

bacteria, but never in their proteins. Similarly, the D-form of glucose is the main product of photosynthesis and the L-form of the molecule is rarely seen in nature.



The functional groups shown here are found in many different biological molecules. Hydrogen bonds connect two strands of DNA together to create the double-helix structure.

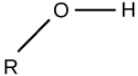
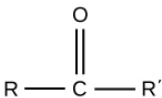
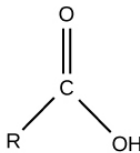
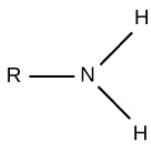
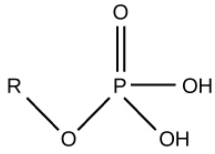
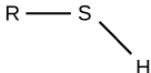
Functional Groups

Functional groups are groups of atoms that occur within molecules and confer specific chemical properties to those molecules. They are found along the “carbon backbone” of macromolecules. This carbon backbone is formed by chains and/or rings of carbon atoms with the occasional substitution of an element such as nitrogen or oxygen. Molecules with other elements in their carbon backbone are **substituted hydrocarbons**.

The functional groups in a macromolecule are usually attached to the carbon backbone at one or several different places along its chain and/or ring structure. Each of the four types of macromolecules—proteins, lipids, carbohydrates, and nucleic acids—has its own characteristic set of functional groups that contributes greatly to its differing chemical properties and its function in living organisms.

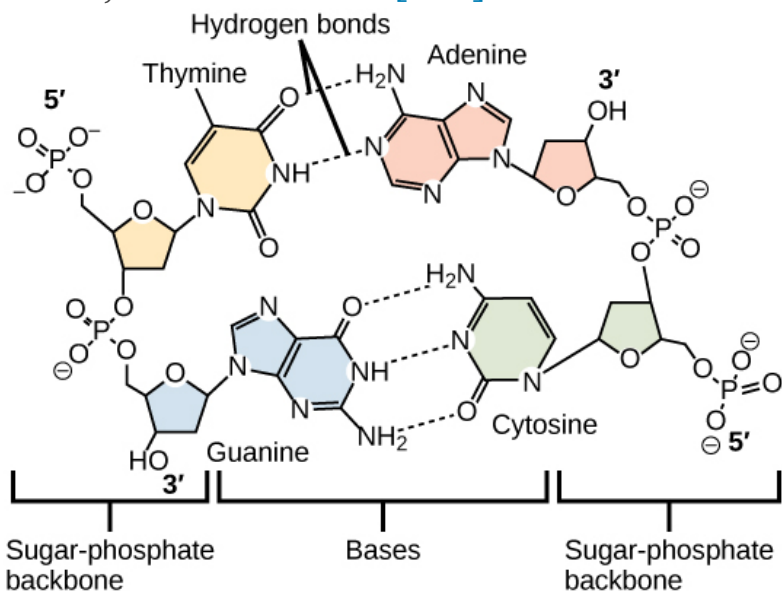
A functional group can participate in specific chemical reactions. Some of the important functional groups in biological molecules are shown in [\[link\]](#); they include: hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl. These groups play an important role in the formation of molecules like DNA, proteins, carbohydrates, and lipids. Functional groups are usually classified as hydrophobic or hydrophilic depending on their charge or polarity characteristics. An example of a hydrophobic group is the non-polar methane molecule. Among the hydrophilic functional groups is the carboxyl group found in amino acids, some amino acid side chains, and the fatty acids that form triglycerides and phospholipids. This carboxyl group ionizes to release hydrogen ions (H^+) from the $COOH$ group resulting in the negatively charged COO^- group; this contributes to the hydrophilic nature of whatever molecule it is found on. Other functional groups, such as the carbonyl group, have a partially negatively charged oxygen atom that may form hydrogen bonds with water molecules,

again making the molecule more hydrophilic.

Functional Group	Structure	Properties
Hydroxyl		Polar
Methyl	$R - CH_3$	Nonpolar
Carbonyl		Polar
Carboxyl		Charged, ionizes to release H^+ . Since carboxyl groups can release H^+ ions into solution, they are considered acidic.
Amino		Charged, accepts H^+ to form NH_3^+ . Since amino groups can remove H^+ from solution, they are considered basic.
Phosphate		Charged, ionizes to release H^+ . Since phosphate groups can release H^+ ions into solution, they are considered acidic.
Sulfhydryl		Polar

Hydrogen bonds between functional groups (within the same molecule or between different molecules) are important to the function of many macromolecules and help them to fold properly into and maintain the appropriate shape for functioning. Hydrogen bonds are also involved in various recognition processes, such as DNA complementary

base pairing and the binding of an enzyme to its substrate, as illustrated in [\[link\]](#).



Section Summary

The unique properties of carbon make it a central part of biological molecules. Carbon binds to oxygen, hydrogen, and nitrogen covalently to form the many molecules important for cellular function. Carbon has four electrons in its outermost shell and can form four bonds. Carbon and hydrogen can form hydrocarbon chains or rings. Functional groups are groups of atoms that confer specific properties to hydrocarbon (or substituted hydrocarbon) chains or rings that define their overall chemical characteristics and function.

Art Connections

[\[link\]](#) Which of the following statements is false?

1. Molecules with the formulas $\text{CH}_3\text{CH}_2\text{COOH}$ and $\text{C}_3\text{H}_6\text{O}_2$ could be structural isomers.
2. Molecules must have a double bond to be *cis-trans* isomers.
3. To be enantiomers, a molecule must have at least three different atoms or groups connected to a central carbon.
4. To be enantiomers, a molecule must have at least four different atoms or groups connected to a central carbon.

[\[link\]](#) C

Review Questions

Each carbon molecule can bond with as many as _____ other atom(s) or molecule(s).

1. one
2. two

3. six
4. four

D

Which of the following is not a functional group that can bond with carbon?

1. sodium
2. hydroxyl
3. phosphate
4. carbonyl

A

Free Response

What property of carbon makes it essential for organic life?

Carbon is unique and found in all living things because it can form up to four covalent bonds between atoms or molecules. These can be nonpolar or polar covalent bonds, and they allow for the formation of long chains of carbon

molecules that combine to form proteins and DNA.

Compare and contrast saturated and unsaturated triglycerides.

Saturated triglycerides contain no double bonds between carbon atoms; they are usually solid at room temperature. Unsaturated triglycerides contain at least one double bond between carbon atoms and are usually liquid at room temperature.

Glossary

aliphatic hydrocarbon

hydrocarbon consisting of a linear chain of carbon atoms

aromatic hydrocarbon

hydrocarbon consisting of closed rings of carbon atoms

enantiomers

molecules that share overall structure and bonding patterns, but differ in how the atoms are three dimensionally placed such that they are mirror images of each other

functional group

group of atoms that provides or imparts a specific function to a carbon skeleton

geometric isomer

isomer with similar bonding patterns differing in the placement of atoms alongside a double covalent bond

hydrocarbon

molecule that consists only of carbon and hydrogen

isomers

molecules that differ from one another even though they share the same chemical formula

organic molecule

any molecule containing carbon (except carbon dioxide)

structural isomers

molecules that share a chemical formula but differ in the placement of their chemical bonds

substituted hydrocarbon

hydrocarbon chain or ring containing an atom of another element in place of one of the backbone carbons

Water

By the end of this section, you will be able to:

- Describe the properties of water that are critical to maintaining life
- Explain why water is an excellent solvent
- Provide examples of water's cohesive and adhesive properties
- Discuss the role of acids, bases, and buffers in homeostasis

Why do scientists spend time looking for water on other planets? Why is water so important? It is because water is essential to life as we know it. Water is one of the more abundant molecules and the one most critical to life on Earth. Approximately 60–70 percent of the human body is made up of water. Without it, life as we know it simply would not exist.

The polarity of the water molecule and its resulting hydrogen bonding make water a unique substance with special properties that are intimately tied to the processes of life. Life originally evolved in a watery environment, and most of an organism's cellular chemistry and metabolism occur inside the watery contents of the cell's cytoplasm. Special properties of water are its high heat capacity and heat of vaporization, its ability to dissolve polar molecules, its cohesive and adhesive properties, and its dissociation into ions that leads to the generation

of pH. Understanding these characteristics of water helps to elucidate its importance in maintaining life.

Oil and water do not mix. As this macro image of oil and water shows, oil does not dissolve in water but forms droplets instead. This is due to it being a nonpolar compound. (credit: Gautam Dogra).

Water's Polarity

One of water's important properties is that it is composed of polar molecules: the hydrogen and oxygen within water molecules (H_2O) form polar covalent bonds. While there is no net charge to a water molecule, the polarity of water creates a slightly positive charge on hydrogen and a slightly negative charge on oxygen, contributing to water's properties of attraction. Water's charges are generated because oxygen is more electronegative than hydrogen, making it more likely that a shared electron would be found near the oxygen nucleus than the hydrogen nucleus, thus generating the partial negative charge near the oxygen.

As a result of water's polarity, each water molecule attracts other water molecules because of the opposite charges between water molecules, forming hydrogen bonds. Water also attracts or is attracted to other polar molecules and ions. A polar substance that interacts readily with or dissolves in water is referred to as **hydrophilic** (hydro- = "water"; -philic = "loving"). In contrast, non-polar molecules

such as oils and fats do not interact well with water, as shown in [\[link\]](#) and separate from it rather than dissolve in it, as we see in salad dressings containing oil and vinegar (an acidic water solution). These nonpolar compounds are called **hydrophobic** (hydro- = “water”; -phobic = “fearing”).



Hydrogen bonding makes ice less dense than liquid water. The (a) lattice structure of ice makes it less dense than the freely flowing molecules of liquid water, enabling it to (b) float on water. (credit a: modification of work by Jane Whitney, image created using Visual Molecular Dynamics (VMD) software^{[\[footnote\]](#)}; credit b: modification of work by Carlos Ponte)W. Humphrey W., A. Dalke, and K. Schulten, “VMD—Visual Molecular Dynamics,” *Journal of Molecular Graphics* 14 (1996): 33-38.

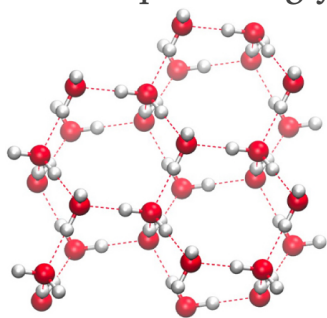
Water's States: Gas, Liquid, and Solid

The formation of hydrogen bonds is an important quality of the liquid water that is crucial to life as we know it. As water molecules make hydrogen bonds with each other, water takes on some unique chemical characteristics compared to other liquids and, since living things have a high water content, understanding these chemical features is key to understanding life. In liquid water, hydrogen bonds are constantly formed and broken as the water molecules slide past each other. The breaking of these bonds is caused by the motion (kinetic energy) of the water molecules due to the heat contained in the system. When the heat is raised as water is boiled, the higher kinetic energy of the water molecules causes the hydrogen bonds to break completely and allows water molecules to escape into the air as gas (steam or water vapor). On the other hand, when the temperature of water is reduced and water freezes, the water molecules form a crystalline structure maintained by hydrogen bonding (there is not enough energy to break the hydrogen bonds) that makes ice less dense than liquid water, a phenomenon not seen in the solidification of other liquids.

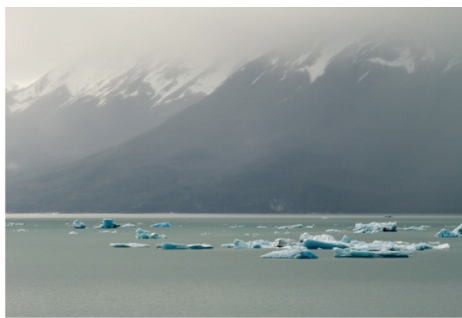
Water's lower density in its solid form is due to the way hydrogen bonds are oriented as it freezes: the water molecules are pushed farther apart compared to liquid water. With most other liquids,

solidification when the temperature drops includes the lowering of kinetic energy between molecules, allowing them to pack even more tightly than in liquid form and giving the solid a greater density than the liquid.

The lower density of ice, illustrated and pictured in [\[link\]](#), an anomaly, causes it to float at the surface of liquid water, such as in an iceberg or in the ice cubes in a glass of ice water. In lakes and ponds, ice will form on the surface of the water creating an insulating barrier that protects the animals and plant life in the pond from freezing. Without this layer of insulating ice, plants and animals living in the pond would freeze in the solid block of ice and could not survive. The detrimental effect of freezing on living organisms is caused by the expansion of ice relative to liquid water. The ice crystals that form upon freezing rupture the delicate membranes essential for the function of living cells, irreversibly damaging them. Cells can only survive freezing if the water in them is temporarily replaced by another liquid like glycerol.



(a)



(b)

Link to Learning



Click [here](#) to see a 3-D animation of the structure of an ice lattice. (Image credit: Jane Whitney. Image created using Visual Molecular Dynamics VMD software.[\[footnote\]](#))

W. Humphrey W., A. Dalke, and K. Schulten, “VMD—Visual Molecular Dynamics,” *Journal of Molecular Graphics* 14 (1996): 33-38.

Water’s High Heat Capacity

Water’s high heat capacity is a property caused by hydrogen bonding among water molecules. Water has the highest **specific heat capacity** of any liquids. Specific heat is defined as the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius. For water, this amount is one **calorie**. It therefore takes water a long time to heat and long time to cool. In

fact, the specific heat capacity of water is about five times more than that of sand. This explains why the land cools faster than the sea. Due to its high heat capacity, water is used by warm blooded animals to more evenly disperse heat in their bodies: it acts in a similar manner to a car's cooling system, transporting heat from warm places to cool places, causing the body to maintain a more even temperature.

Water's Heat of Vaporization

Water also has a high **heat of vaporization**, the amount of energy required to change one gram of a liquid substance to a gas. A considerable amount of heat energy (586 cal) is required to accomplish this change in water. This process occurs on the surface of water. As liquid water heats up, hydrogen bonding makes it difficult to separate the liquid water molecules from each other, which is required for it to enter its gaseous phase (steam). As a result, water acts as a heat sink or heat reservoir and requires much more heat to boil than does a liquid such as ethanol (grain alcohol), whose hydrogen bonding with other ethanol molecules is weaker than water's hydrogen bonding. Eventually, as water reaches its boiling point of 100° Celsius (212° Fahrenheit), the heat is able to break the hydrogen bonds between the water molecules, and the kinetic energy (motion) between the water molecules

allows them to escape from the liquid as a gas. Even when below its boiling point, water's individual molecules acquire enough energy from other water molecules such that some surface water molecules can escape and vaporize: this process is known as **evaporation**.

The fact that hydrogen bonds need to be broken for water to evaporate means that a substantial amount of energy is used in the process. As the water evaporates, energy is taken up by the process, cooling the environment where the evaporation is taking place. In many living organisms, including in humans, the evaporation of sweat, which is 90 percent water, allows the organism to cool so that homeostasis of body temperature can be maintained.

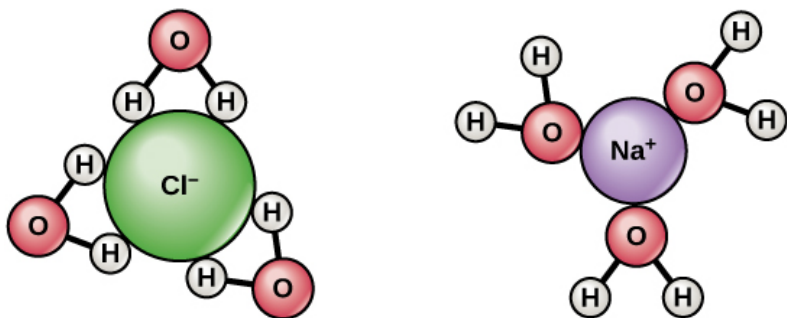
When table salt (NaCl) is mixed in water, spheres of hydration are formed around the ions.

Water's Solvent Properties

Since water is a polar molecule with slightly positive and slightly negative charges, ions and polar molecules can readily dissolve in it. Therefore, water is referred to as a **solvent**, a substance capable of dissolving other polar molecules and ionic compounds. The charges associated with these molecules will form hydrogen bonds with water, surrounding the particle with water molecules. This is referred to as a **sphere of hydration**, or a

hydration shell, as illustrated in [\[link\]](#) and serves to keep the particles separated or dispersed in the water.

When ionic compounds are added to water, the individual ions react with the polar regions of the water molecules and their ionic bonds are disrupted in the process of **dissociation**. Dissociation occurs when atoms or groups of atoms break off from molecules and form ions. Consider table salt (NaCl, or sodium chloride): when NaCl crystals are added to water, the molecules of NaCl dissociate into Na^+ and Cl^- ions, and spheres of hydration form around the ions, illustrated in [\[link\]](#). The positively charged sodium ion is surrounded by the partially negative charge of the water molecule's oxygen. The negatively charged chloride ion is surrounded by the partially positive charge of the hydrogen on the water molecule.



The weight of the needle is pulling the surface downward; at the same time, the surface tension is pulling it up, suspending it on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit:

Cory Zanker) Capillary action in a glass tube is caused by the adhesive forces exerted by the internal surface of the glass exceeding the cohesive forces between the water molecules themselves.

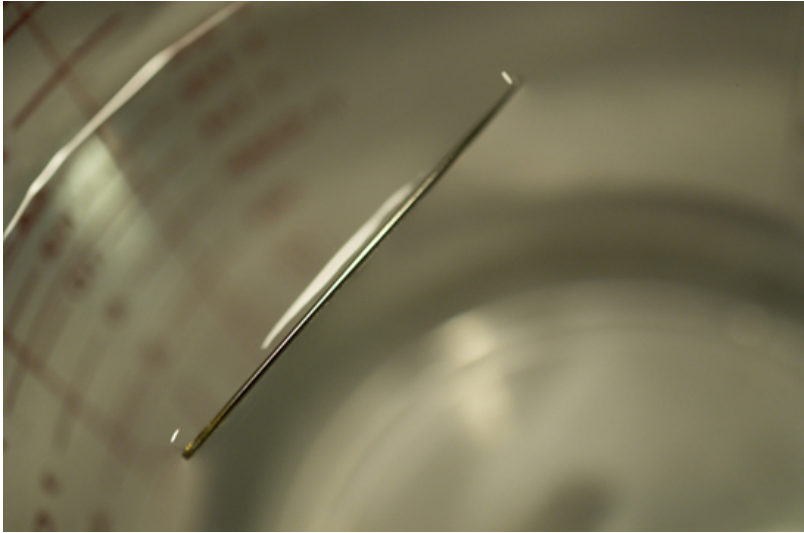
(credit: modification of work by Pearson-Scott Foresman, donated to the Wikimedia Foundation) Water's cohesive and adhesive properties allow this water strider (*Gerris* sp.) to stay afloat. (credit: Tim Vickers)

Water's Cohesive and Adhesive Properties

Have you ever filled a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of **cohesion**. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-gas (water-air) interface, although there is no more room in the glass.

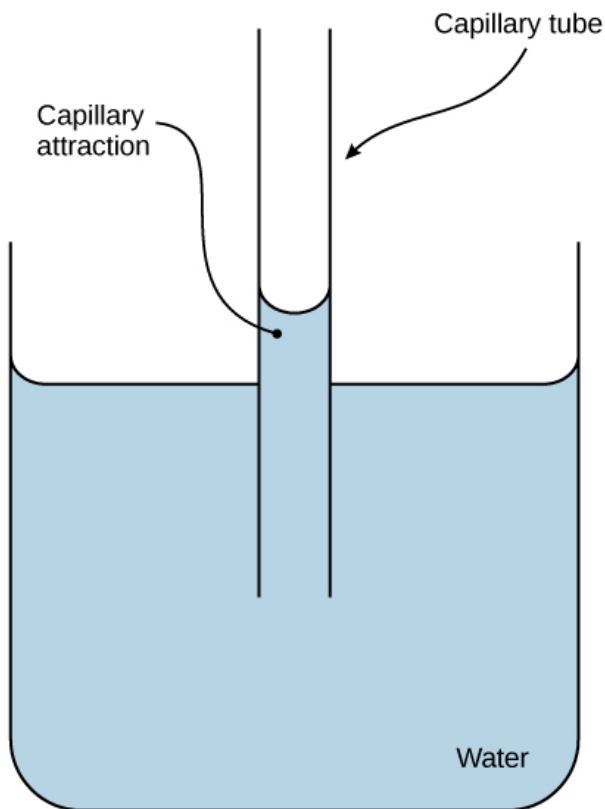
Cohesion allows for the development of **surface tension**, the capacity of a substance to withstand being ruptured when placed under tension or stress. This is also why water forms droplets when placed on a dry surface rather than being flattened out by gravity. When a small scrap of paper is placed onto the droplet of water, the paper floats on top of the water droplet even though paper is denser (heavier)

than the water. Cohesion and surface tension keep the hydrogen bonds of water molecules intact and support the item floating on the top. It's even possible to “float” a needle on top of a glass of water if it is placed gently without breaking the surface tension, as shown in [\[link\]](#).



These cohesive forces are related to water's property of **adhesion**, or the attraction between water molecules and other molecules. This attraction is sometimes stronger than water's cohesive forces, especially when the water is exposed to charged surfaces such as those found on the inside of thin glass tubes known as capillary tubes. Adhesion is observed when water “climbs” up the tube placed in a glass of water: notice that the water appears to be higher on the sides of the tube than in the middle. This is because the water molecules are attracted to the charged glass walls of the capillary more than they are to each other and therefore adhere to it.

This type of adhesion is called **capillary action**, and is illustrated in [\[link\]](#).



Why are cohesive and adhesive forces important for life? Cohesive and adhesive forces are important for the transport of water from the roots to the leaves in plants. These forces create a “pull” on the water column. This pull results from the tendency of water molecules being evaporated on the surface of the plant to stay connected to water molecules below them, and so they are pulled along. Plants use this natural phenomenon to help transport water from their roots to their leaves. Without these properties

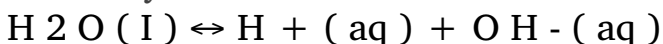
of water, plants would be unable to receive the water and the dissolved minerals they require. In another example, insects such as the water strider, shown in [\[link\]](#), use the surface tension of water to stay afloat on the surface layer of water and even mate there.



The pH scale measures the concentration of hydrogen ions (H^+) in a solution. (credit: modification of work by Edward Stevens) This diagram shows the body's buffering of blood pH levels. The blue arrows show the process of raising pH as more CO_2 is made. The purple arrows indicate the reverse process: the lowering of pH as more bicarbonate is created.

pH, Buffers, Acids, and Bases

The pH of a solution indicates its acidity or alkalinity.



litmus or pH paper, filter paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid (acidity) or base (alkalinity) exists in a solution. You might have even used some to test whether the water in a swimming pool is properly treated. In both cases, the pH test measures the concentration of hydrogen ions in a given solution.

Hydrogen ions are spontaneously generated in pure water by the dissociation (ionization) of a small percentage of water molecules into equal numbers of hydrogen (H^+) ions and hydroxide (OH^-) ions. While the hydroxide ions are kept in solution by their hydrogen bonding with other water molecules, the hydrogen ions, consisting of naked protons, are immediately attracted to un-ionized water molecules, forming hydronium ions (H_3O^+). Still, by convention, scientists refer to hydrogen ions and their concentration as if they were free in this state in liquid water.

The concentration of hydrogen ions dissociating from pure water is 1×10^{-7} moles H^+ ions per liter of water. Moles (mol) are a way to express the amount of a substance (which can be atoms, molecules, ions, etc), with one mole being equal to 6.02×10^{23} particles of the substance. Therefore, 1 mole of water is equal to 6.02×10^{23} water molecules. The pH is calculated as the negative of the base 10 logarithm of this concentration. The

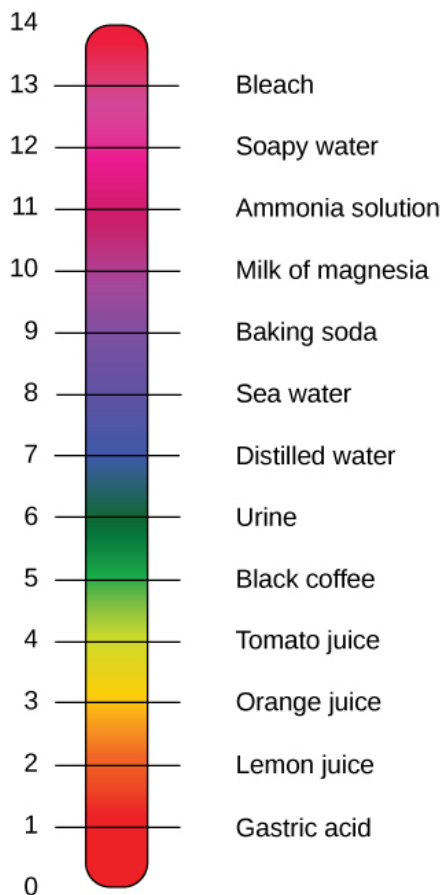
\log_{10} of 1×10^{-7} is -7.0, and the negative of this number (indicated by the “p” of “pH”) yields a pH of 7.0, which is also known as neutral pH. The pH inside of human cells and blood are examples of two areas of the body where near-neutral pH is maintained.

Non-neutral pH readings result from dissolving acids or bases in water. Using the negative logarithm to generate positive integers, high concentrations of hydrogen ions yield a low pH number, whereas low levels of hydrogen ions result in a high pH. An **acid** is a substance that increases the concentration of hydrogen ions (H^+) in a solution, usually by having one of its hydrogen atoms dissociate. A **base** provides either hydroxide ions (OH^-) or other negatively charged ions that combine with hydrogen ions, reducing their concentration in the solution and thereby raising the pH. In cases where the base releases hydroxide ions, these ions bind to free hydrogen ions, generating new water molecules.

The stronger the acid, the more readily it donates H^+ . For example, hydrochloric acid (HCl) completely dissociates into hydrogen and chloride ions and is highly acidic, whereas the acids in tomato juice or vinegar do not completely dissociate and are considered weak acids. Conversely, strong bases are those substances that readily donate OH^- or take up hydrogen ions. Sodium hydroxide ($NaOH$) and many household cleaners are highly alkaline and give up

OH^- rapidly when placed in water, thereby raising the pH. An example of a weak basic solution is seawater, which has a pH near 8.0, close enough to neutral pH that marine organisms adapted to this saline environment are able to thrive in it.

The **pH scale** is, as previously mentioned, an inverse logarithm and ranges from 0 to 14 ([\[link\]](#)). Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. Extremes in pH in either direction from 7.0 are usually considered inhospitable to life. The pH inside cells (6.8) and the pH in the blood (7.4) are both very close to neutral. However, the environment in the stomach is highly acidic, with a pH of 1 to 2. So how do the cells of the stomach survive in such an acidic environment? How do they homeostatically maintain the near neutral pH inside them? The answer is that they cannot do it and are constantly dying. New stomach cells are constantly produced to replace dead ones, which are digested by the stomach acids. It is estimated that the lining of the human stomach is completely replaced every seven to ten days.



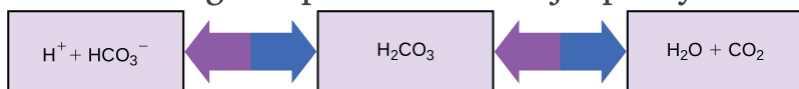
Link to Learning



Watch this video for a straightforward explanation of pH and its logarithmic scale.

https://www.openstaxcollege.org/l/pH_scale

So how can organisms whose bodies require a near-neutral pH ingest acidic and basic substances (a human drinking orange juice, for example) and survive? Buffers are the key. **Buffers** readily absorb excess H^+ or OH^- , keeping the pH of the body carefully maintained in the narrow range required for survival. Maintaining a constant blood pH is critical to a person's well-being. The buffer maintaining the pH of human blood involves carbonic acid (H_2CO_3), bicarbonate ion (HCO_3^-), and carbon dioxide (CO_2). When bicarbonate ions combine with free hydrogen ions and become carbonic acid, hydrogen ions are removed, moderating pH changes. Similarly, as shown in [\[link\]](#), excess carbonic acid can be converted to carbon dioxide gas and exhaled through the lungs. This prevents too many free hydrogen ions from building up in the blood and dangerously reducing the blood's pH. Likewise, if too much OH^- is introduced into the system, carbonic acid will combine with it to create bicarbonate, lowering the pH. Without this buffer system, the body's pH would fluctuate enough to put survival in jeopardy.



Other examples of buffers are antacids used to combat excess stomach acid. Many of these over-the-counter medications work in the same way as blood buffers, usually with at least one ion capable of absorbing hydrogen and moderating pH, bringing relief to those that suffer “heartburn” after eating. The unique properties of water that contribute to this capacity to balance pH—as well as water’s other characteristics—are essential to sustaining life on Earth.

Link to Learning



To learn more about water. Visit the [U.S. Geological Survey Water Science for Schools All About Water! website](#).

Section Summary

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds. Hydrogen bonds allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules cause the water to have a high heat capacity, meaning it takes a lot of added heat to raise its temperature. As the temperature rises, the hydrogen bonds between water continually break and form anew. This allows for the overall temperature to remain stable, although energy is added to the system. Water also exhibits a high heat of vaporization, which is key to how organisms cool themselves by the evaporation of sweat. Water's cohesive forces allow for the property of surface tension, whereas its adhesive properties are seen as water rises inside capillary tubes. The pH value is a measure of hydrogen ion concentration in a solution and is one of many chemical characteristics that is highly regulated in living organisms through homeostasis. Acids and bases can change pH values, but buffers tend to moderate the changes they cause. These properties of water are intimately connected to the biochemical and physical processes performed by living organisms, and life would be very different if these properties were altered, if it could exist at all.

Review Questions

Which of the following statements is not true?

1. Water is polar.
2. Water stabilizes temperature.
3. Water is essential for life.
4. Water is the most abundant molecule in the Earth's atmosphere.

D

When acids are added to a solution, the pH should _____.

1. decrease
2. increase
3. stay the same
4. cannot tell without testing

A

A molecule that binds up excess hydrogen ions in a solution is called a(n) _____.

1. acid
 2. isotope
 3. base
 4. donator
-

C

Which of the following statements is true?

1. Acids and bases cannot mix together.
2. Acids and bases will neutralize each other.
3. Acids, but not bases, can change the pH of a solution.
4. Acids donate hydroxide ions (OH^-); bases donate hydrogen ions (H^+).

B

Free Response

Discuss how buffers help prevent drastic swings in pH.

Buffers absorb the free hydrogen ions and hydroxide ions that result from chemical reactions. Because they can bond these ions, they prevent increases or decreases in pH. An example of a buffer system is the bicarbonate system in the human body. This system is able to absorb hydrogen and hydroxide ions to

prevent changes in pH and keep cells functioning properly.

Why can some insects walk on water?

Some insects can walk on water, although they are heavier (denser) than water, because of the surface tension of water. Surface tension results from cohesion, or the attraction between water molecules at the surface of the body of water (the liquid-air/gas interface).

Glossary

acid

molecule that donates hydrogen ions and increases the concentration of hydrogen ions in a solution

adhesion

attraction between water molecules and other molecules

base

molecule that donates hydroxide ions or otherwise binds excess hydrogen ions and decreases the concentration of hydrogen ions in a solution

buffer

substance that prevents a change in pH by absorbing or releasing hydrogen or hydroxide ions

calorie

amount of heat required to change the temperature of one gram of water by one degree Celsius

capillary action

occurs because water molecules are attracted to charges on the inner surfaces of narrow tubular structures such as glass tubes, drawing the water molecules to the sides of the tubes

cohesion

intermolecular forces between water molecules caused by the polar nature of water; responsible for surface tension

dissociation

release of an ion from a molecule such that the original molecule now consists of an ion and the charged remains of the original, such as when water dissociates into H^+ and OH^-

evaporation

separation of individual molecules from the surface of a body of water, leaves of a plant, or the skin of an organism

heat of vaporization of water

high amount of energy required for liquid water to turn into water vapor

hydrophilic

describes ions or polar molecules that interact well with other polar molecules such as water

hydrophobic

describes uncharged non-polar molecules that do not interact well with polar molecules such as water

litmus paper

(also, pH paper) filter paper that has been treated with a natural water-soluble dye that changes its color as the pH of the environment changes so it can be used as a pH indicator

pH paper

see litmus paper

pH scale

scale ranging from zero to 14 that is inversely proportional to the concentration of hydrogen ions in a solution

solvent

substance capable of dissolving another substance

specific heat capacity

the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius

sphere of hydration

when a polar water molecule surrounds charged or polar molecules thus keeping them dissolved and in solution

surface tension

tension at the surface of a body of liquid that prevents the molecules from separating; created by the attractive cohesive forces between the molecules of the liquid

Proteins

By the end of this section, you will be able to:

- Describe the functions proteins perform in the cell and in tissues
- Discuss the relationship between amino acids and proteins
- Explain the four levels of protein organization
- Describe the ways in which protein shape and function are linked

Proteins are one of the most abundant organic molecules in living systems and have the most diverse range of functions of all macromolecules. Proteins may be structural, regulatory, contractile, or protective; they may serve in transport, storage, or membranes; or they may be toxins or enzymes. Each cell in a living system may contain thousands of proteins, each with a unique function. Their structures, like their functions, vary greatly. They are all, however, polymers of amino acids, arranged in a linear sequence.

Types and Functions of Proteins

Enzymes, which are produced by living cells, are catalysts in biochemical reactions (like digestion) and are usually complex or conjugated proteins. Each enzyme is specific for the substrate (a reactant

that binds to an enzyme) it acts on. The enzyme may help in breakdown, rearrangement, or synthesis reactions. Enzymes that break down their substrates are called catabolic enzymes, enzymes that build more complex molecules from their substrates are called anabolic enzymes, and enzymes that affect the rate of reaction are called catalytic enzymes. It should be noted that all enzymes increase the rate of reaction and, therefore, are considered to be organic catalysts. An example of an enzyme is salivary amylase, which hydrolyzes its substrate amylose, a component of starch.

Hormones are chemical-signaling molecules, usually small proteins or steroids, secreted by endocrine cells that act to control or regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that helps to regulate the blood glucose level. The primary types and functions of proteins are listed in [\[link\]](#).

Protein Types and Functions		
Type	Examples	Functions
Digestive Enzymes	Amylase, lipase, pepsin, trypsin	Help in digestion of food by

			catabolizing nutrients into monomeric units
Transport	Hemoglobin, albumin		Carry substances in the blood or lymph throughout the body
Structural	Actin, tubulin, keratin		Construct different structures, like the cytoskeleton
Hormones	Insulin, thyroxine		Coordinate the activity of different body systems
Defense	Immunoglobulins		Protect the body from foreign pathogens
Contractile	Actin, myosin		Effect muscle contraction
Storage	Legume storage proteins, egg white (albumin)		Provide nourishment in early development of the embryo and the seedling

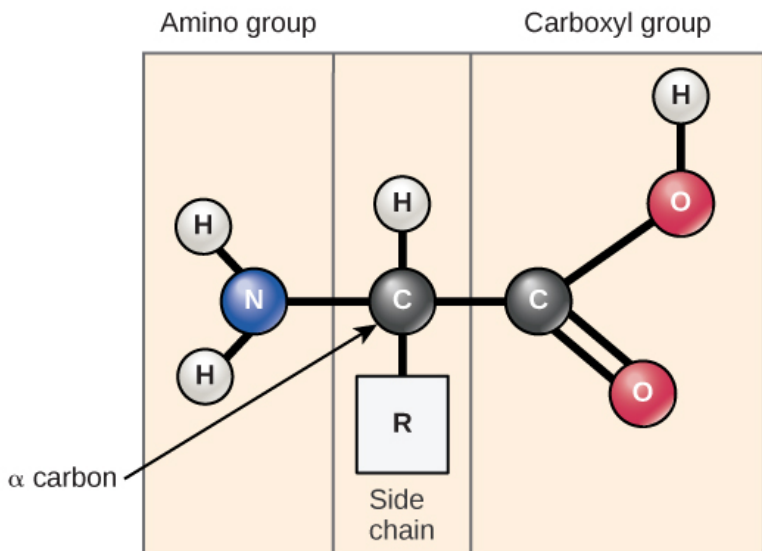
Proteins have different shapes and molecular weights; some proteins are globular in shape whereas others are fibrous in nature. For example,

hemoglobin is a globular protein, but collagen, found in our skin, is a fibrous protein. Protein shape is critical to its function, and this shape is maintained by many different types of chemical bonds. Changes in temperature, pH, and exposure to chemicals may lead to permanent changes in the shape of the protein, leading to loss of function, known as **denaturation**. All proteins are made up of different arrangements of the same 20 types of amino acids.

Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached. Peptide bond formation is a dehydration synthesis reaction. The carboxyl group of one amino acid is linked to the amino group of the incoming amino acid. In the process, a molecule of water is released.

Amino Acids

Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom, also known as the alpha (α) carbon, bonded to an amino group (NH_2), a carboxyl group (COOH), and to a hydrogen atom. Every amino acid also has another atom or group of atoms bonded to the central atom known as the R group ([\[link\]](#)).



The name "amino acid" is derived from the fact that they contain both amino group and carboxyl-acid-group in their basic structure. As mentioned, there are 20 amino acids present in proteins. Nine of these are considered essential amino acids in humans because the human body cannot produce them and they are obtained from the diet. For each amino acid, the R group (or side chain) is different ([\[link\]](#)).

Art Connection

There are 20 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature.

AMINO ACID			
Nonpolar, aliphatic R groups	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{H} \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_3 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH} \\ \quad \\ \text{CH}_3 \quad \text{CH}_3 \end{array}$
	Glycine	Alanine	Valine
	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH} \\ \quad \\ \text{CH}_3 \quad \text{CH}_3 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{S} \\ \\ \text{CH}_3 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{H} - \text{C} - \text{CH}_3 \\ \\ \text{CH}_2 \\ \\ \text{CH}_3 \end{array}$
	Leucine	Methionine	Isoleucine
Polar, uncharged R groups	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2\text{OH} \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{H} - \text{C} - \text{OH} \\ \\ \text{CH}_3 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{SH} \end{array}$
	Serine	Threonine	Cysteine
	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_2\text{N}^+ - \text{C} - \text{H} \\ \quad \\ \text{H}_2\text{C} - \text{CH}_2 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{C} \\ \quad \\ \text{H}_2\text{N} \quad \text{O} \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{C} \\ \quad \\ \text{H}_2\text{N} \quad \text{O} \end{array}$
	Proline	Asparagine	Glutamine
AMINO ACID			
Positively charged R groups	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{NH}_3^+ \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{NH} \\ \\ \text{C} = \text{NH}_2 \\ \\ \text{NH}_2 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{C} - \text{NH}^+ \\ \quad \\ \text{C} = \text{N} \\ \quad \\ \text{H} \quad \text{CH} \end{array}$
	Lysine	Arginine	Histidine
Negatively charged R groups	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{COO}^- \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{CH}_2 \\ \\ \text{COO}^- \end{array}$	
	Aspartate	Glutamate	
Nonpolar, aromatic R groups	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{C}_6\text{H}_5 \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{C}_6\text{H}_4\text{OH} \end{array}$	$\begin{array}{c} \text{COO}^- \\ \\ \text{H}_3\text{N}^+ - \text{C} - \text{H} \\ \\ \text{CH}_2 \\ \\ \text{C}_8\text{H}_6\text{N} \end{array}$
	Phenylalanine	Tyrosine	Tryptophan

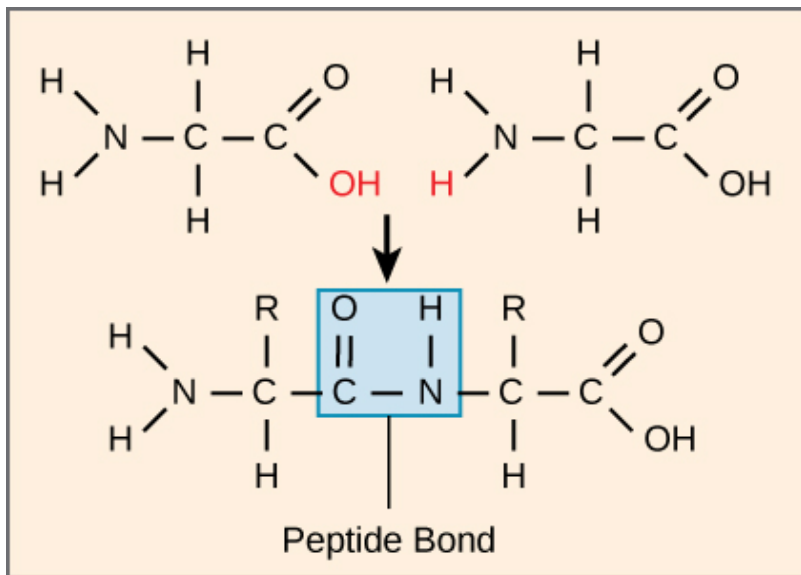
Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

The chemical nature of the side chain determines the nature of the amino acid (that is, whether it is acidic, basic, polar, or nonpolar). For example, the amino acid glycine has a hydrogen atom as the R group. Amino acids such as valine, methionine, and alanine are nonpolar or hydrophobic in nature, while amino acids such as serine, threonine, and

cysteine are polar and have hydrophilic side chains. The side chains of lysine and arginine are positively charged, and therefore these amino acids are also known as basic amino acids. Proline has an R group that is linked to the amino group, forming a ring-like structure. Proline is an exception to the standard structure of an amino acid since its amino group is not separate from the side chain ([\[link\]](#)).

Amino acids are represented by a single upper case letter or a three-letter abbreviation. For example, valine is known by the letter V or the three-letter symbol val. Just as some fatty acids are essential to a diet, some amino acids are necessary as well. They are known as essential amino acids, and in humans they include isoleucine, leucine, and cysteine. Essential amino acids refer to those necessary for construction of proteins in the body, although not produced by the body; which amino acids are essential varies from organism to organism.

The sequence and the number of amino acids ultimately determine the protein's shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a **peptide bond**, which is formed by a dehydration reaction. The carboxyl group of one amino acid and the amino group of the incoming amino acid combine, releasing a molecule of water. The resulting bond is the peptide bond ([\[link\]](#)).



The products formed by such linkages are called peptides. As more amino acids join to this growing chain, the resulting chain is known as a polypeptide. Each polypeptide has a free amino group at one end. This end is called the N terminal, or the amino terminal, and the other end has a free carboxyl group, also known as the C or carboxyl terminal. While the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically a polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have combined together, often have bound non-peptide prosthetic groups, have a distinct shape, and have a unique function. After protein synthesis (translation), most proteins are modified. These are known as post-translational modifications. They may undergo cleavage, phosphorylation, or may require the addition of

other chemical groups. Only after these modifications is the protein completely functional.

Link to Learning



Click through the steps of protein synthesis in this [interactive tutorial](#).

Evolution Connection

The Evolutionary Significance of Cytochrome c

Cytochrome c is an important component of the electron transport chain, a part of cellular respiration, and it is normally found in the cellular organelle, the mitochondrion. This protein has a heme prosthetic group, and the central ion of the heme gets alternately reduced and oxidized during electron transfer. Because this essential protein's role in producing cellular energy is crucial, it has

changed very little over millions of years. Protein sequencing has shown that there is a considerable amount of cytochrome c amino acid sequence homology among different species; in other words, evolutionary kinship can be assessed by measuring the similarities or differences among various species' DNA or protein sequences.

Scientists have determined that human cytochrome c contains 104 amino acids. For each cytochrome c molecule from different organisms that has been sequenced to date, 37 of these amino acids appear in the same position in all samples of cytochrome c. This indicates that there may have been a common ancestor. On comparing the human and chimpanzee protein sequences, no sequence difference was found. When human and rhesus monkey sequences were compared, the single difference found was in one amino acid. In another comparison, human to yeast sequencing shows a difference in the 44th position.

Bovine serum insulin is a protein hormone made of two peptide chains, A (21 amino acids long) and B (30 amino acids long). In each chain, primary structure is indicated by three-letter abbreviations that represent the names of the amino acids in the order they are present. The amino acid cysteine (cys) has a sulfhydryl (SH) group as a side chain. Two sulfhydryl groups can react in the presence of

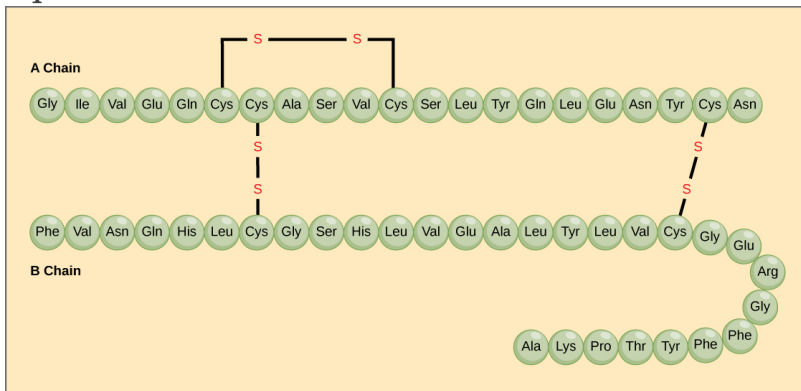
oxygen to form a disulfide (S-S) bond. Two disulfide bonds connect the A and B chains together, and a third helps the A chain fold into the correct shape. Note that all disulfide bonds are the same length, but are drawn different sizes for clarity. The beta chain of hemoglobin is 147 residues in length, yet a single amino acid substitution leads to sickle cell anemia. In normal hemoglobin, the amino acid at position seven is glutamate. In sickle cell hemoglobin, this glutamate is replaced by a valine. In this blood smear, visualized at 535x magnification using bright field microscopy, sickle cells are crescent shaped, while normal cells are disc-shaped. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)The α -helix and β -pleated sheet are secondary structures of proteins that form because of hydrogen bonding between carbonyl and amino groups in the peptide backbone. Certain amino acids have a propensity to form an α -helix, while others have a propensity to form a β -pleated sheet. The tertiary structure of proteins is determined by a variety of chemical interactions. These include hydrophobic interactions, ionic bonding, hydrogen bonding and disulfide linkages. The four levels of protein structure can be observed in these illustrations. (credit: modification of work by National Human Genome Research Institute)

Protein Structure

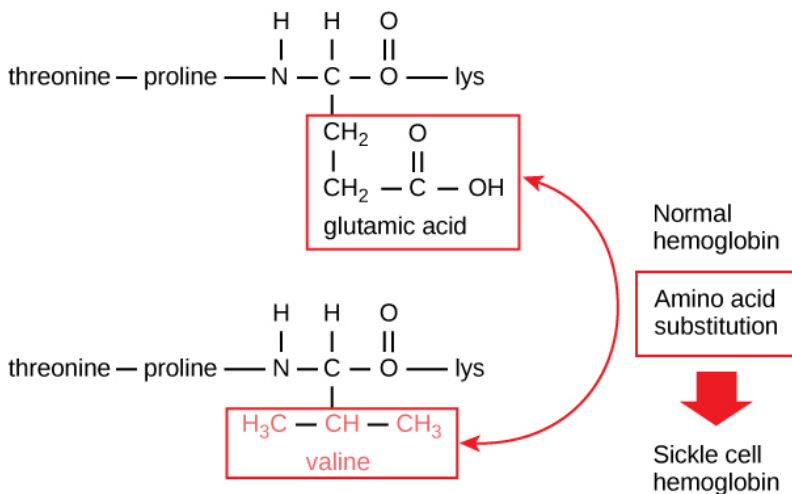
As discussed earlier, the shape of a protein is critical to its function. For example, an enzyme can bind to a specific substrate at a site known as the active site. If this active site is altered because of local changes or changes in overall protein structure, the enzyme may be unable to bind to the substrate. To understand how the protein gets its final shape or conformation, we need to understand the four levels of protein structure: primary, secondary, tertiary, and quaternary.

Primary Structure

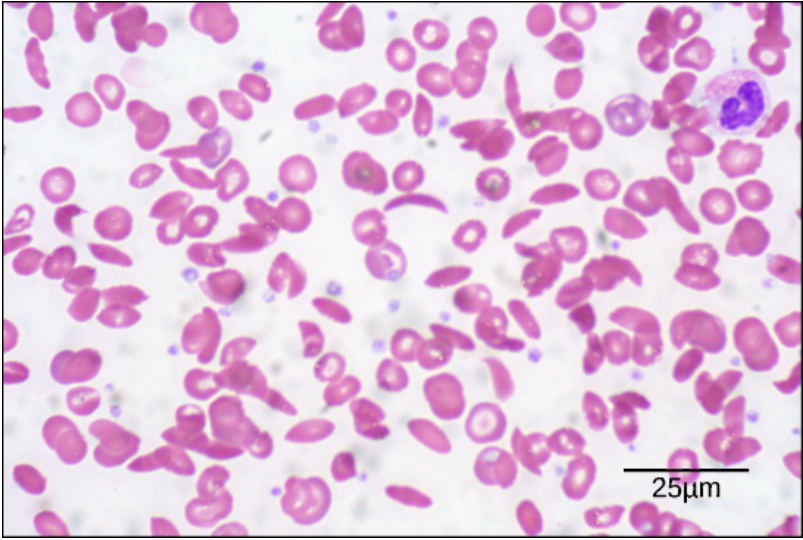
The unique sequence of amino acids in a polypeptide chain is its **primary structure**. For example, the pancreatic hormone insulin has two polypeptide chains, A and B, and they are linked together by disulfide bonds. The N terminal amino acid of the A chain is glycine, whereas the C terminal amino acid is asparagine ([link]). The sequences of amino acids in the A and B chains are unique to insulin.



The unique sequence for every protein is ultimately determined by the gene encoding the protein. A change in nucleotide sequence of the gene's coding region may lead to a different amino acid being added to the growing polypeptide chain, causing a change in protein structure and function. In sickle cell anemia, the hemoglobin β chain (a small portion of which is shown in [\[link\]](#)) has a single amino acid substitution, causing a change in protein structure and function. Specifically, the amino acid glutamic acid is substituted by valine in the β chain. What is most remarkable to consider is that a hemoglobin molecule is made up of two alpha chains and two beta chains that each consist of about 150 amino acids. The molecule, therefore, has about 600 amino acids. The structural difference between a normal hemoglobin molecule and a sickle cell molecule—which dramatically decreases life expectancy—is a single amino acid of the 600. What is even more remarkable is that those 600 amino acids are encoded by three nucleotides each, and the mutation is caused by a single base change (point mutation), 1 in 1800 bases.



Because of this change of one amino acid in the chain, hemoglobin molecules form long fibers that distort the biconcave, or disc-shaped, red blood cells and assume a crescent or “sickle” shape, which clogs arteries ([\[link\]](#)). This can lead to myriad serious health problems such as breathlessness, dizziness, headaches, and abdominal pain for those affected by this disease.



Secondary Structure

The local folding of the polypeptide in some regions gives rise to the **secondary structure** of the protein. The most common are the **α -helix** and **β -pleated sheet** structures ([\[link\]](#)). Both structures are the α -helix structure—the helix held in shape by hydrogen bonds. The hydrogen bonds form between the oxygen atom in the carbonyl group in one amino acid and another amino acid that is four amino acids farther along the chain.

The diagram illustrates the three major types of secondary protein structure:

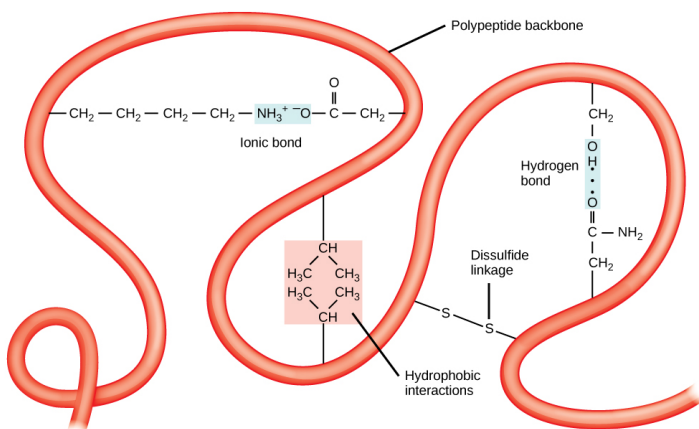
- α-helix:** A coiled ribbon structure, shown in green, with a side chain (Val, His, Thr) attached. An arrow indicates the direction of the polypeptide chain.
- β-pleated sheet:** A zigzag ribbon structure, shown in blue. An arrow indicates the direction of the polypeptide chain.
- Loop:** A curved ribbon structure, shown in blue, connecting different parts of the protein chain.

Below the main structures, the chemical structures of the repeating units are shown:

- α-helix:** A coiled ribbon structure, shown in green, with a side chain (Val, His, Thr) attached. An arrow indicates the direction of the polypeptide chain.
- β-pleated sheet:** A zigzag ribbon structure, shown in blue. An arrow indicates the direction of the polypeptide chain.
- Loop:** A curved ribbon structure, shown in blue, connecting different parts of the protein chain.

Tertiary Structure

The unique three-dimensional structure of a polypeptide is its **tertiary structure** ([\[link\]](#)). This structure is in part due to chemical interactions at work on the polypeptide chain. Primarily, the interactions among R groups creates the complex three-dimensional tertiary structure of a protein. The nature of the R groups found in the amino acids involved can counteract the formation of the hydrogen bonds described for standard secondary structures. For example, R groups with like charges are repelled by each other and those with unlike charges are attracted to each other (ionic bonds). When protein folding takes place, the hydrophobic R groups of nonpolar amino acids lay in the interior of the protein, whereas the hydrophilic R groups lay on the outside. The former types of interactions are also known as hydrophobic interactions. Interaction between cysteine side chains forms disulfide linkages in the presence of oxygen, the only covalent bond forming during protein folding.

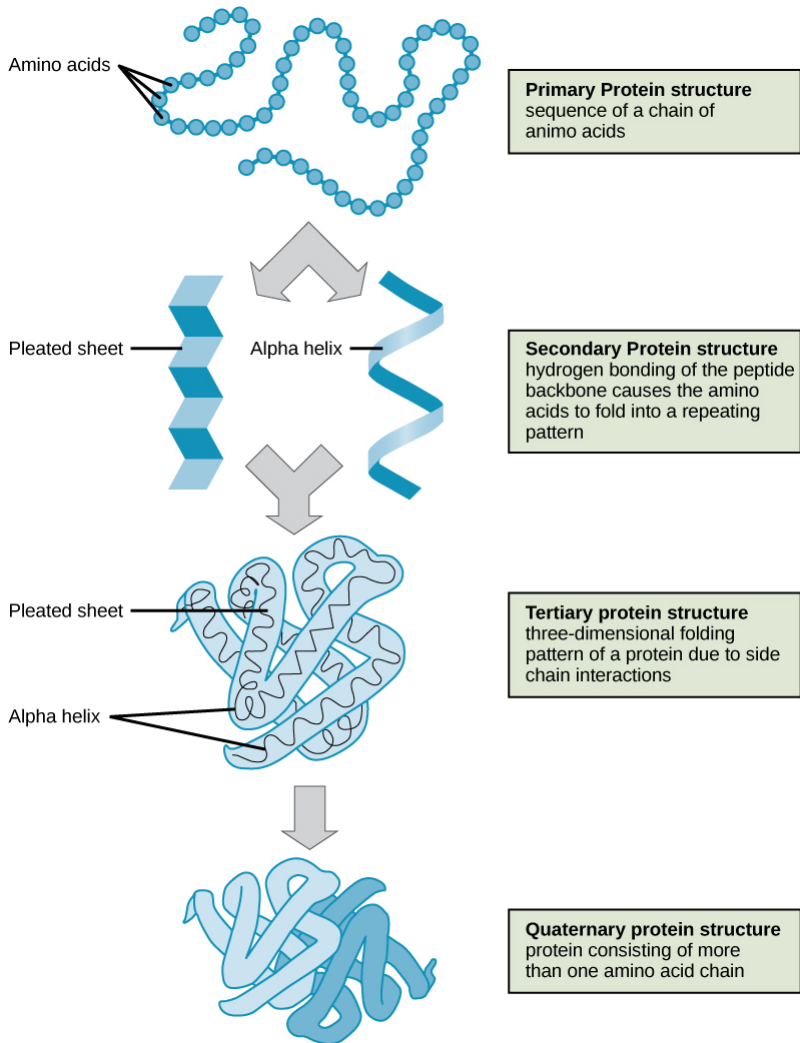


All of these interactions, weak and strong, determine the final three-dimensional shape of the protein. When a protein loses its three-dimensional shape, it may no longer be functional.

Quaternary Structure

In nature, some proteins are formed from several polypeptides, also known as subunits, and the interaction of these subunits forms the **quaternary structure**. Weak interactions between the subunits help to stabilize the overall structure. For example, insulin (a globular protein) has a combination of hydrogen bonds and disulfide bonds that cause it to be mostly clumped into a ball shape. Insulin starts out as a single polypeptide and loses some internal sequences in the presence of post-translational modification after the formation of the disulfide linkages that hold the remaining chains together. Silk (a fibrous protein), however, has a β -pleated sheet structure that is the result of hydrogen bonding between different chains.

The four levels of protein structure (primary, secondary, tertiary, and quaternary) are illustrated in [\[link\]](#).



Denaturation and Protein Folding

Each protein has its own unique sequence and shape that are held together by chemical interactions. If the protein is subject to changes in temperature, pH,

or exposure to chemicals, the protein structure may change, losing its shape without losing its primary sequence in what is known as denaturation.

Denaturation is often reversible because the primary structure of the polypeptide is conserved in the process if the denaturing agent is removed, allowing the protein to resume its function. Sometimes denaturation is irreversible, leading to loss of function. One example of irreversible protein denaturation is when an egg is fried. The albumin protein in the liquid egg white is denatured when placed in a hot pan. Not all proteins are denatured at high temperatures; for instance, bacteria that survive in hot springs have proteins that function at temperatures close to boiling. The stomach is also very acidic, has a low pH, and denatures proteins as part of the digestion process; however, the digestive enzymes of the stomach retain their activity under these conditions.

Protein folding is critical to its function. It was originally thought that the proteins themselves were responsible for the folding process. Only recently was it found that often they receive assistance in the folding process from protein helpers known as **chaperones** (or chaperonins) that associate with the target protein during the folding process. They act by preventing aggregation of polypeptides that make up the complete protein structure, and they disassociate from the protein once the target protein is folded.

Link to Learning



For an additional perspective on proteins, view [this animation](#) called “Biomolecules: The Proteins.”

Section Summary

Proteins are a class of macromolecules that perform a diverse range of functions for the cell. They help in metabolism by providing structural support and by acting as enzymes, carriers, or hormones. The building blocks of proteins (monomers) are amino acids. Each amino acid has a central carbon that is linked to an amino group, a carboxyl group, a hydrogen atom, and an R group or side chain. There are 20 commonly occurring amino acids, each of which differs in the R group. Each amino acid is linked to its neighbors by a peptide bond. A long chain of amino acids is known as a polypeptide.

Proteins are organized at four levels: primary, secondary, tertiary, and (optional) quaternary. The primary structure is the unique sequence of amino acids. The local folding of the polypeptide to form structures such as the α helix and β -pleated sheet constitutes the secondary structure. The overall three-dimensional structure is the tertiary structure. When two or more polypeptides combine to form the complete protein structure, the configuration is known as the quaternary structure of a protein. Protein shape and function are intricately linked; any change in shape caused by changes in temperature or pH may lead to protein denaturation and a loss in function.

Art Connections

[\[link\]](#) Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

[\[link\]](#) Polar and charged amino acid residues (the remainder after peptide bond formation) are more likely to be found on the surface of

soluble proteins where they can interact with water, and nonpolar (e.g., amino acid side chains) are more likely to be found in the interior where they are sequestered from water. In membrane proteins, nonpolar and hydrophobic amino acid side chains associate with the hydrophobic tails of phospholipids, while polar and charged amino acid side chains interact with the polar head groups or with the aqueous solution. However, there are exceptions. Sometimes, positively and negatively charged amino acid side chains interact with one another in the interior of a protein, and polar or charged amino acid side chains that interact with a ligand can be found in the ligand binding pocket.

Review Questions

The monomers that make up proteins are called _____.

1. nucleotides
 2. disaccharides
 3. amino acids
 4. chaperones
-

C

The α helix and the β -pleated sheet are part of which protein structure?

1. primary
2. secondary
3. tertiary
4. quaternary

B

Free Response

Explain what happens if even one amino acid is substituted for another in a polypeptide chain. Provide a specific example.

A change in gene sequence can lead to a different amino acid being added to a polypeptide chain instead of the normal one. This causes a change in protein structure and function. For example, in sickle cell anemia, the hemoglobin β chain has a single amino acid substitution—the amino acid glutamic acid in

position six is substituted by valine. Because of this change, hemoglobin molecules form aggregates, and the disc-shaped red blood cells assume a crescent shape, which results in serious health problems.

Describe the differences in the four protein structures.

The sequence and number of amino acids in a polypeptide chain is its primary structure. The local folding of the polypeptide in some regions is the secondary structure of the protein. The three-dimensional structure of a polypeptide is known as its tertiary structure, created in part by chemical interactions such as hydrogen bonds between polar side chains, van der Waals interactions, disulfide linkages, and hydrophobic interactions. Some proteins are formed from multiple polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure.

Glossary

alpha-helix structure (α -helix)

type of secondary structure of proteins formed by folding of the polypeptide into a helix shape with hydrogen bonds stabilizing

the structure

amino acid

monomer of a protein; has a central carbon or alpha carbon to which an amino group, a carboxyl group, a hydrogen, and an R group or side chain is attached; the R group is different for all 20 amino acids

beta-pleated sheet (β -pleated)

secondary structure found in proteins in which “pleats” are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain

chaperone

(also, chaperonin) protein that helps nascent protein in the folding process

denaturation

loss of shape in a protein as a result of changes in temperature, pH, or exposure to chemicals

enzyme

catalyst in a biochemical reaction that is usually a complex or conjugated protein

hormone

chemical signaling molecule, usually protein or steroid, secreted by endocrine cells that act to control or regulate specific physiological

processes

peptide bond

bond formed between two amino acids by a dehydration reaction

polypeptide

long chain of amino acids linked by peptide bonds

primary structure

linear sequence of amino acids in a protein

protein

biological macromolecule composed of one or more chains of amino acids

quaternary structure

association of discrete polypeptide subunits in a protein

secondary structure

regular structure formed by proteins by intramolecular hydrogen bonding between the oxygen atom of one amino acid residue and the hydrogen attached to the nitrogen atom of another amino acid residue

tertiary structure

three-dimensional conformation of a protein, including interactions between secondary structural elements; formed from interactions

between amino acid side chains

Carbohydrates

By the end of this section, you will be able to:

- Discuss the role of carbohydrates in cells and in the extracellular materials of animals and plants
- Explain the classifications of carbohydrates
- List common monosaccharides, disaccharides, and polysaccharides

Most people are familiar with carbohydrates, one type of macromolecule, especially when it comes to what we eat. To lose weight, some individuals adhere to “low-carb” diets. Athletes, in contrast, often “carb-load” before important competitions to ensure that they have enough energy to compete at a high level. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Carbohydrates provide energy to the body, particularly through glucose, a simple sugar that is a component of **starch** and an ingredient in many staple foods. Carbohydrates also have other important functions in humans, animals, and plants.

Monosaccharides are classified based on the position of their carbonyl group and the number of carbons in the backbone. Aldoses have a carbonyl group (indicated in green) at the end of the carbon chain, and ketoses have a carbonyl group in the middle of the carbon chain. Trioses, pentoses, and hexoses have three, five, and six carbon backbones,

respectively. Five and six carbon monosaccharides exist in equilibrium between linear and ring forms. When the ring forms, the side chain it closes on is locked into an α or β position. Fructose and ribose also form rings, although they form five-membered rings as opposed to the six-membered ring of glucose. Sucrose is formed when a monomer of glucose and a monomer of fructose are joined in a dehydration reaction to form a glycosidic bond. In the process, a water molecule is lost. By convention, the carbon atoms in a monosaccharide are numbered from the terminal carbon closest to the carbonyl group. In sucrose, a glycosidic linkage is formed between carbon 1 in glucose and carbon 2 in fructose. Common disaccharides include maltose (grain sugar), lactose (milk sugar), and sucrose (table sugar). Amylose and amylopectin are two different forms of starch. Amylose is composed of unbranched chains of glucose monomers connected by α 1,4 glycosidic linkages. Amylopectin is composed of branched chains of glucose monomers connected by α 1,4 and α 1,6 glycosidic linkages. Because of the way the subunits are joined, the glucose chains have a helical structure. Glycogen (not shown) is similar in structure to amylopectin but more highly branched. In cellulose, glucose monomers are linked in unbranched chains by β 1-4 glycosidic linkages. Because of the way the glucose subunits are joined, every glucose monomer is flipped relative to the next one resulting in a linear, fibrous structure. Insects have a hard outer

exoskeleton made of chitin, a type of polysaccharide. (credit: Louise Docker)

Molecular Structures

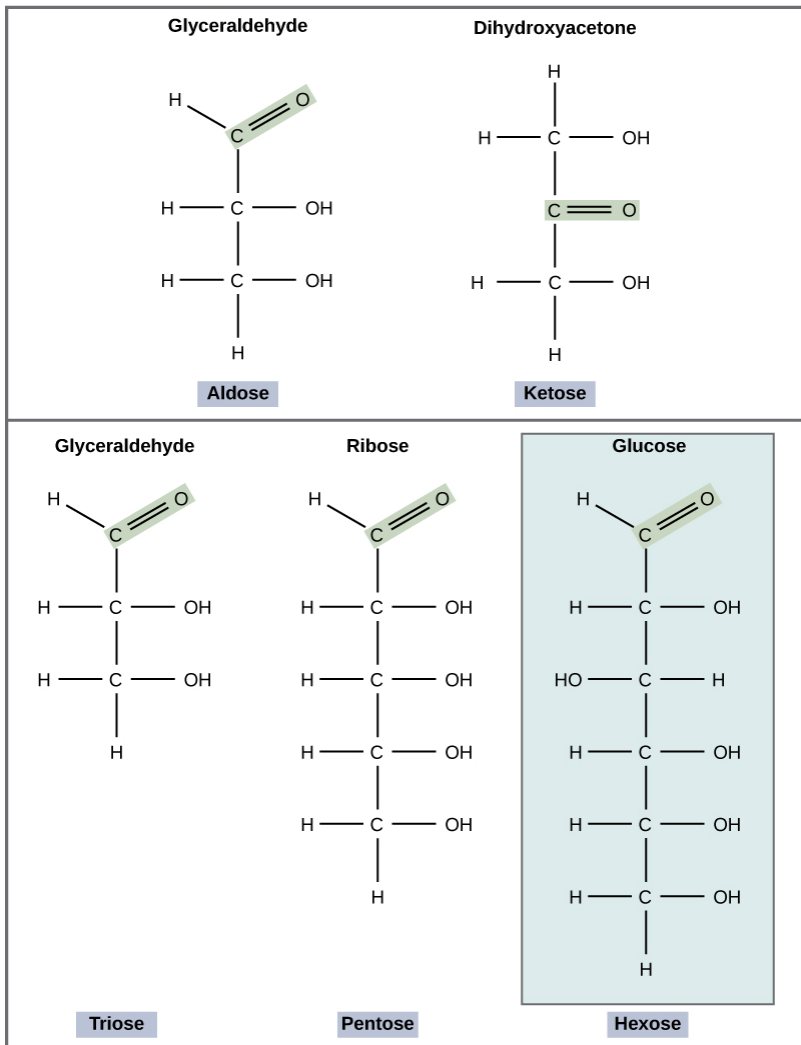
Carbohydrates can be represented by the stoichiometric formula $(\text{CH}_2\text{O})_n$, where n is the number of carbons in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. This formula also explains the origin of the term “carbohydrate”: the components are carbon (“carbo”) and the components of water (hence, “hydrate”). Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

Monosaccharides

Monosaccharides (mono- = “one”; sacchar- = “sweet”) are simple sugars, the most common of which is glucose. In monosaccharides, the number of carbons usually ranges from three to seven. Most monosaccharide names end with the suffix -ose. If the sugar has an aldehyde group (the functional group with the structure R-CHO), it is known as an aldose, and if it has a ketone group (the functional group with the structure RC(=O)R'), it is known as a ketose. Depending on the number of carbons in the sugar, they also may be known as trioses (three

carbons), pentoses (five carbons), and or hexoses (six carbons). See [\[link\]](#) for an illustration of the monosaccharides.

MONOSACCHARIDES



The chemical formula for glucose is $C_6H_{12}O_6$. In humans, glucose is an important source of energy. During cellular respiration, energy is released from

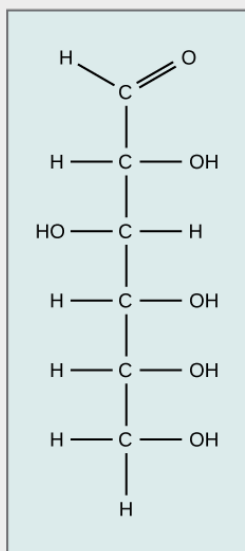
glucose, and that energy is used to help make adenosine triphosphate (ATP). Plants synthesize glucose using carbon dioxide and water, and glucose in turn is used for energy requirements for the plant. Excess glucose is often stored as starch that is catabolized (the breakdown of larger molecules by cells) by humans and other animals that feed on plants.

Galactose (part of lactose, or milk sugar) and fructose (found in sucrose, in fruit) are other common monosaccharides. Although glucose, galactose, and fructose all have the same chemical formula ($C_6H_{12}O_6$), they differ structurally and chemically (and are known as isomers) because of the different arrangement of functional groups around the asymmetric carbon; all of these monosaccharides have more than one asymmetric carbon ([\[link\]](#)).

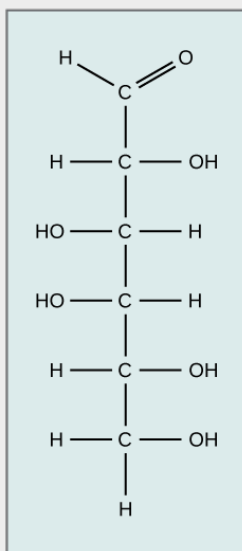
Art Connection

Glucose, galactose, and fructose are all hexoses. They are structural isomers, meaning they have the same chemical formula ($C_6H_{12}O_6$) but a different arrangement of atoms.

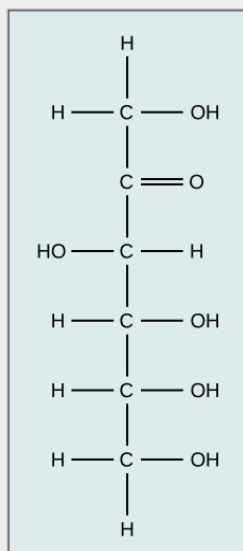
Glucose



Galactose



Fructose

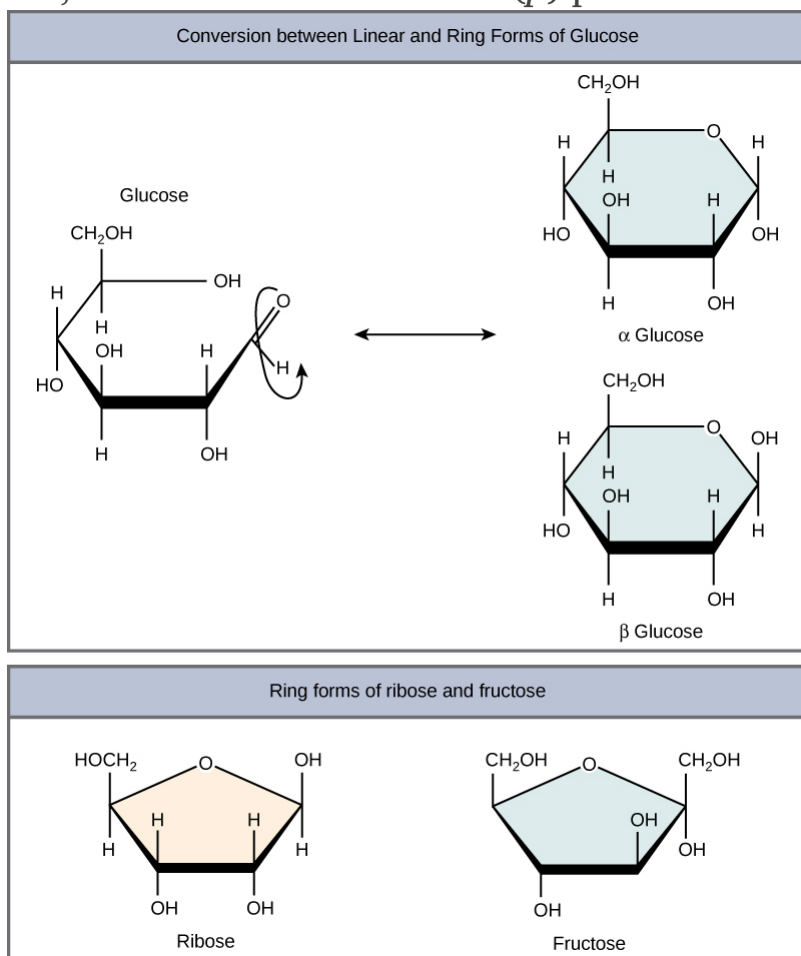


What kind of sugars are these, aldose or ketose?

Glucose, galactose, and fructose are isomeric monosaccharides (hexoses), meaning they have the same chemical formula but have slightly different structures. Glucose and galactose are aldoses, and fructose is a ketose.

Monosaccharides can exist as a linear chain or as ring-shaped molecules; in aqueous solutions they are usually found in ring forms ([\[link\]](#)). Glucose in a ring form can have two different arrangements of the hydroxyl group (OH) around the anomeric carbon (carbon 1 that becomes asymmetric in the process of ring formation). If the hydroxyl group is below carbon number 1 in the sugar, it is said to be

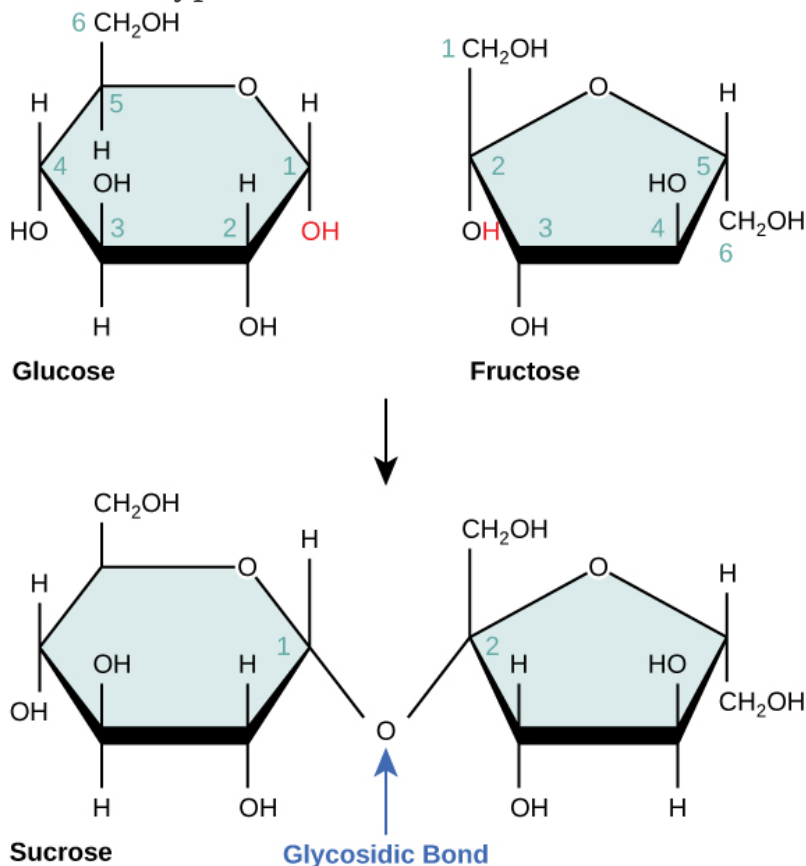
in the alpha (α) position, and if it is above the plane, it is said to be in the beta (β) position.



Disaccharides

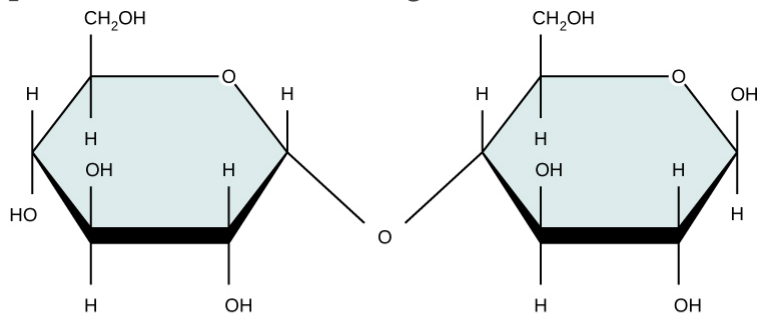
Disaccharides (di- = “two”) form when two monosaccharides undergo a dehydration reaction (also known as a condensation reaction or dehydration synthesis). During this process, the hydroxyl group of one monosaccharide combines

with the hydrogen of another monosaccharide, releasing a molecule of water and forming a covalent bond. A covalent bond formed between a carbohydrate molecule and another molecule (in this case, between two monosaccharides) is known as a **glycosidic bond** ([\[link\]](#)). Glycosidic bonds (also called glycosidic linkages) can be of the alpha or the beta type.

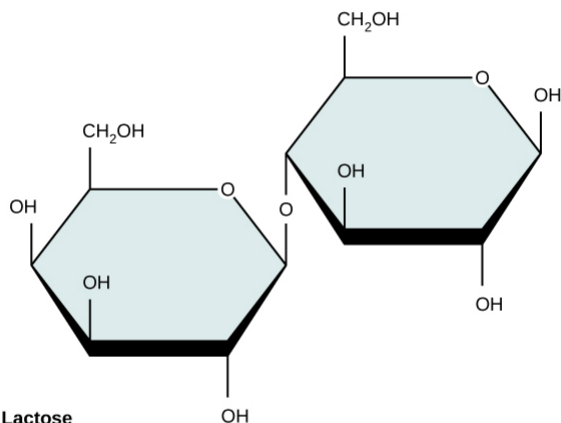


Common disaccharides include lactose, maltose, and sucrose ([\[link\]](#)). Lactose is a disaccharide consisting of the monomers glucose and galactose. It is found

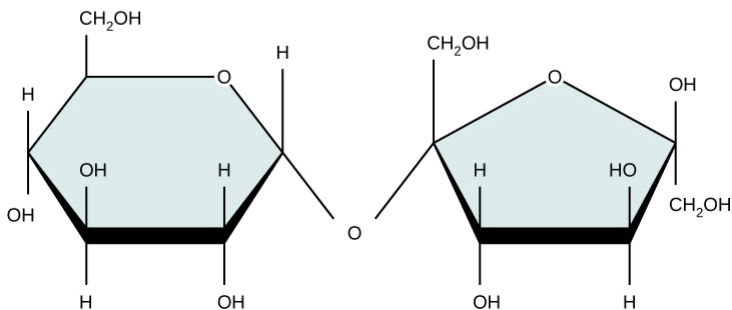
naturally in milk. Maltose, or malt sugar, is a disaccharide formed by a dehydration reaction between two glucose molecules. The most common disaccharide is sucrose, or table sugar, which is composed of the monomers glucose and fructose.



Maltose



Lactose



Sucrose

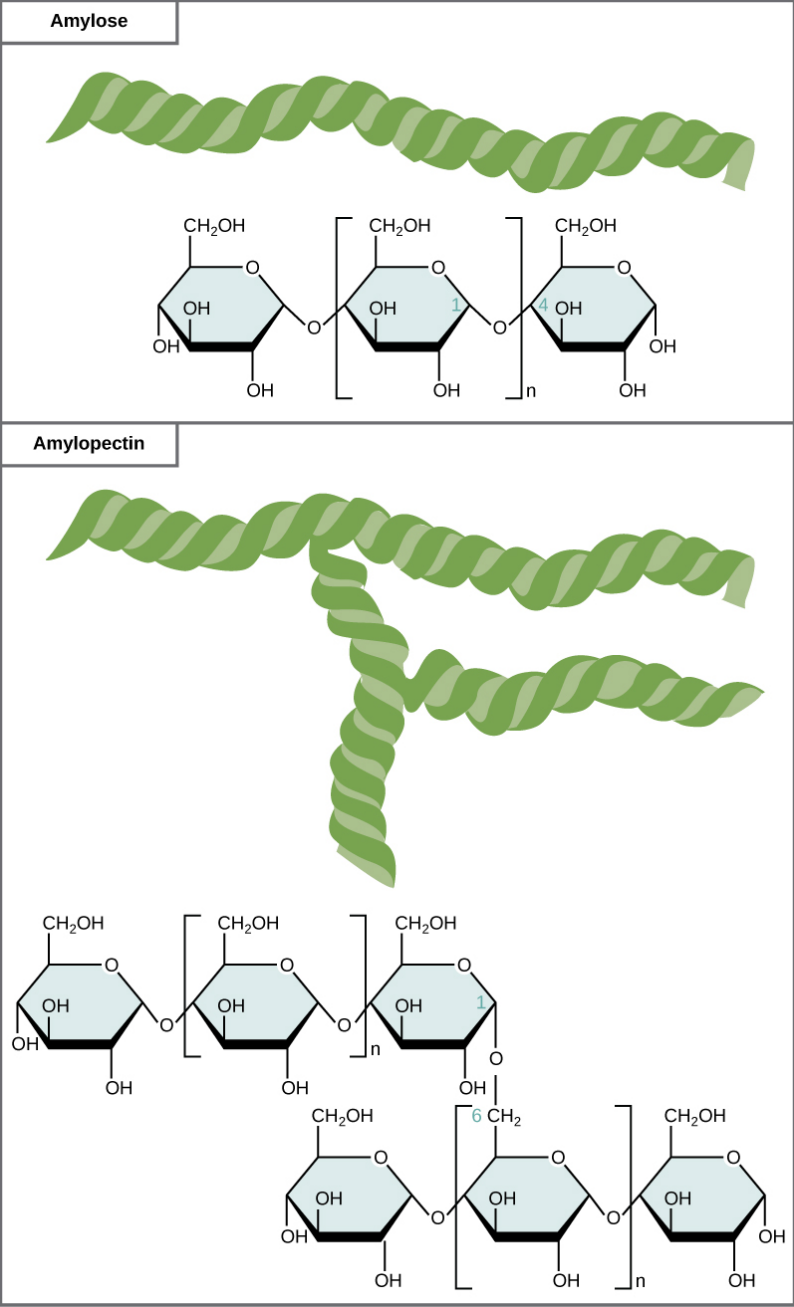
Polysaccharides

A long chain of monosaccharides linked by glycosidic bonds is known as a **polysaccharide** (poly- = “many”). The chain may be branched or unbranched, and it may contain different types of monosaccharides. The molecular weight may be 100,000 daltons or more depending on the number of monomers joined. Starch, glycogen, cellulose, and chitin are primary examples of polysaccharides.

Starch is the stored form of sugars in plants and is made up of a mixture of amylose and amylopectin (both polymers of glucose). Plants are able to synthesize glucose, and the excess glucose, beyond the plant's immediate energy needs, is stored as starch in different plant parts, including roots and seeds. The starch in the seeds provides food for the embryo as it germinates and can also act as a source of food for humans and animals. The starch that is consumed by humans is broken down by enzymes, such as salivary amylases, into smaller molecules, such as maltose and glucose. The cells can then absorb the glucose.

Starch is made up of glucose monomers that are joined by α 1-4 or α 1-6 glycosidic bonds. The numbers 1-4 and 1-6 refer to the carbon number of the two residues that have joined to form the bond. As illustrated in [\[link\]](#), amylose is starch formed by unbranched chains of glucose monomers (only α 1-4

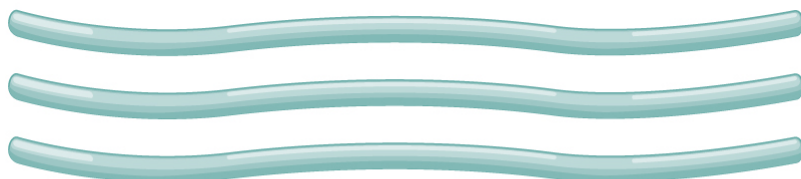
linkages), whereas amylopectin is a branched polysaccharide (α 1-6 linkages at the branch points).



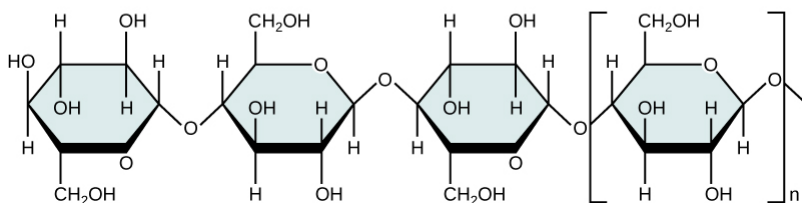
Glycogen is the storage form of glucose in humans and other vertebrates and is made up of monomers of glucose. Glycogen is the animal equivalent of starch and is a highly branched molecule usually stored in liver and muscle cells. Whenever blood glucose levels decrease, glycogen is broken down to release glucose in a process known as glycogenolysis.

Cellulose is the most abundant natural biopolymer. The cell wall of plants is mostly made of cellulose; this provides structural support to the cell. Wood and paper are mostly cellulosic in nature. Cellulose is made up of glucose monomers that are linked by β 1-4 glycosidic bonds ([\[link\]](#)).

Cellulose fibers



Cellulose structure



As shown in [\[link\]](#), every other glucose monomer in cellulose is flipped over, and the monomers are packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—

which is so important to plant cells. While the β 1-4 linkage cannot be broken down by human digestive enzymes, herbivores such as cows, koalas, and buffalos are able, with the help of the specialized flora in their stomach, to digest plant material that is rich in cellulose and use it as a food source. In these animals, certain species of bacteria and protists reside in the rumen (part of the digestive system of herbivores) and secrete the enzyme cellulase. The appendix of grazing animals also contains bacteria that digest cellulose, giving it an important role in the digestive systems of ruminants. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal. Termites are also able to break down cellulose because of the presence of other organisms in their bodies that secrete cellulases.

Carbohydrates serve various functions in different animals. Arthropods (insects, crustaceans, and others) have an outer skeleton, called the exoskeleton, which protects their internal body parts (as seen in the bee in [\[link\]](#)). This exoskeleton is made of the biological macromolecule **chitin**, which is a polysaccharide-containing nitrogen. It is made of repeating units of N-acetyl- β -d-glucosamine, a modified sugar. Chitin is also a major component of fungal cell walls; fungi are neither animals nor plants and form a kingdom of their own in the domain Eukarya.



Career Connections

Registered Dietitian

Obesity is a worldwide health concern, and many diseases such as diabetes and heart disease are becoming more prevalent because of obesity. This is one of the reasons why registered dietitians are increasingly sought after for advice. Registered dietitians help plan nutrition programs for individuals in various settings. They often work with patients in health care facilities, designing nutrition plans to treat and prevent diseases. For example, dietitians may teach a patient with diabetes how to manage blood sugar levels by

eating the correct types and amounts of carbohydrates. Dietitians may also work in nursing homes, schools, and private practices.

To become a registered dietitian, one needs to earn at least a bachelor's degree in dietetics, nutrition, food technology, or a related field. In addition, registered dietitians must complete a supervised internship program and pass a national exam.

Those who pursue careers in dietetics take courses in nutrition, chemistry, biochemistry, biology, microbiology, and human physiology. Dietitians must become experts in the chemistry and physiology (biological functions) of food (proteins, carbohydrates, and fats).

Benefits of Carbohydrates

Are carbohydrates good for you? People who wish to lose weight are often told that carbohydrates are bad for them and should be avoided. Some diets completely forbid carbohydrate consumption, claiming that a low-carbohydrate diet helps people to lose weight faster. However, carbohydrates have been an important part of the human diet for thousands of years; artifacts from ancient civilizations show the presence of wheat, rice, and corn in our ancestors' storage areas.

Carbohydrates should be supplemented with proteins, vitamins, and fats to be parts of a well-balanced diet. Calorie-wise, a gram of carbohydrate provides 4.3 Kcal. For comparison, fats provide 9 Kcal/g, a less desirable ratio. Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which is mostly cellulose. Fiber has many uses; it promotes regular bowel movement by adding bulk, and it regulates the rate of consumption of blood glucose. Fiber also helps to remove excess cholesterol from the body: fiber binds to the cholesterol in the small intestine, then attaches to the cholesterol and prevents the cholesterol particles from entering the bloodstream, and then cholesterol exits the body via the feces. Fiber-rich diets also have a protective role in reducing the occurrence of colon cancer. In addition, a meal containing whole grains and vegetables gives a feeling of fullness. As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces ATP, the energy currency of the cell. Without the consumption of carbohydrates, the availability of “instant energy” would be reduced. Eliminating carbohydrates from the diet is not the best way to lose weight. A low-calorie diet that is rich in whole grains, fruits, vegetables, and lean meat, together with plenty of exercise and plenty of water, is the more sensible way to lose weight.

Link to Learning



For an additional perspective on carbohydrates, explore “Biomolecules: the Carbohydrates” through this [interactive animation](#).

Section Summary

Carbohydrates are a group of macromolecules that are a vital energy source for the cell and provide structural support to plant cells, fungi, and all of the arthropods that include lobsters, crabs, shrimp, insects, and spiders. Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides depending on the number of monomers in the molecule. Monosaccharides are linked by glycosidic bonds that are formed as a result of dehydration reactions, forming disaccharides and polysaccharides with the

elimination of a water molecule for each bond formed. Glucose, galactose, and fructose are common monosaccharides, whereas common disaccharides include lactose, maltose, and sucrose. Starch and glycogen, examples of polysaccharides, are the storage forms of glucose in plants and animals, respectively. The long polysaccharide chains may be branched or unbranched. Cellulose is an example of an unbranched polysaccharide, whereas amylopectin, a constituent of starch, is a highly branched molecule. Storage of glucose, in the form of polymers like starch or glycogen, makes it slightly less accessible for metabolism; however, this prevents it from leaking out of the cell or creating a high osmotic pressure that could cause excessive water uptake by the cell.

Art Connections

[\[link\]](#) What kind of sugars are these, aldose or ketose?

[\[link\]](#) Glucose and galactose are aldoses. Fructose is a ketose.

Review Questions

An example of a monosaccharide is _____.

1. fructose
2. glucose
3. galactose
4. all of the above

D

Cellulose and starch are examples of:

1. monosaccharides
2. disaccharides
3. lipids
4. polysaccharides

D

Plant cell walls contain which of the following in abundance?

1. starch
2. cellulose
3. glycogen
4. lactose

B

Lactose is a disaccharide formed by the formation of a _____ bond between glucose and _____.

1. glycosidic; lactose
2. glycosidic; galactose
3. hydrogen; sucrose
4. hydrogen; fructose

B

Free Response

Describe the similarities and differences between glycogen and starch.

Glycogen and starch are polysaccharides. They are the storage form of glucose. Glycogen is stored in animals in the liver and in muscle cells, whereas starch is stored in the roots, seeds, and leaves of plants. Starch has two different forms, one unbranched (amylose) and one branched (amylopectin), whereas glycogen

is a single type of a highly branched molecule.

Why is it impossible for humans to digest food that contains cellulose?

The β 1-4 glycosidic linkage in cellulose cannot be broken down by human digestive enzymes. Herbivores such as cows, koalas, and buffalos are able to digest grass that is rich in cellulose and use it as a food source because bacteria and protists in their digestive systems, especially in the rumen, secrete the enzyme cellulase. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal.

Glossary

carbohydrate

biological macromolecule in which the ratio of carbon to hydrogen and to oxygen is 1:2:1; carbohydrates serve as energy sources and structural support in cells and form the a cellular exoskeleton of arthropods

cellulose

polysaccharide that makes up the cell wall of plants; provides structural support to the cell

chitin

type of carbohydrate that forms the outer skeleton of all arthropods that include crustaceans and insects; it also forms the cell walls of fungi

disaccharide

two sugar monomers that are linked together by a glycosidic bond

glycogen

storage carbohydrate in animals

glycosidic bond

bond formed by a dehydration reaction between two monosaccharides with the elimination of a water molecule

monosaccharide

single unit or monomer of carbohydrates

polysaccharide

long chain of monosaccharides; may be branched or unbranched

starch

storage carbohydrate in plants

Lipids

By the end of this section, you will be able to:

- Describe the four major types of lipids
- Explain the role of fats in storing energy
- Differentiate between saturated and unsaturated fatty acids
- Describe phospholipids and their role in cells
- Define the basic structure of a steroid and some functions of steroids
- Explain how cholesterol helps to maintain the fluid nature of the plasma membrane

Lipids include a diverse group of compounds that are largely nonpolar in nature. This is because they are hydrocarbons that include mostly nonpolar carbon–carbon or carbon–hydrogen bonds. Non-polar molecules are hydrophobic (“water fearing”), or insoluble in water. Lipids perform many different functions in a cell. Cells store energy for long-term use in the form of fats. Lipids also provide insulation from the environment for plants and animals ([\[link\]](#)). For example, they help keep aquatic birds and mammals dry when forming a protective layer over fur or feathers because of their water-repellant hydrophobic nature. Lipids are also the building blocks of many hormones and are an important constituent of all cellular membranes. Lipids include fats, oils, waxes, phospholipids, and steroids. Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the

elements. (credit: Ken Bosma)



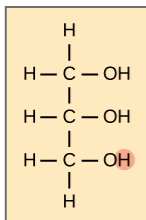
Triacylglycerol is formed by the joining of three fatty acids to a glycerol backbone in a dehydration reaction. Three molecules of water are released in the process. Stearic acid is a common saturated fatty acid. Oleic acid is a common unsaturated fatty acid. Saturated fatty acids have hydrocarbon chains connected by single bonds only. Unsaturated fatty acids have one or more double bonds. Each double bond may be in a *cis* or *trans* configuration. In the *cis* configuration, both hydrogens are on the same side of the hydrocarbon chain. In the *trans* configuration, the hydrogens are on opposite sides. A *cis* double bond causes a kink in the chain. Alpha-linolenic acid is an example of an omega-3 fatty

acid. It has three *cis* double bonds and, as a result, a curved shape. For clarity, the carbons are not shown. Each singly bonded carbon has two hydrogens associated with it, also not shown.

Fats and Oils

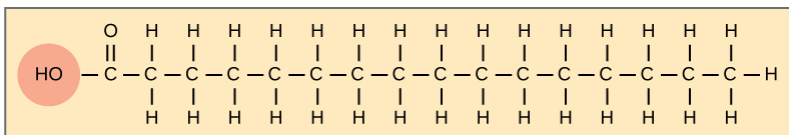
A fat molecule consists of two main components—glycerol and fatty acids. Glycerol is an organic compound (alcohol) with three carbons, five hydrogens, and three hydroxyl (OH) groups. Fatty acids have a long chain of hydrocarbons to which a carboxyl group is attached, hence the name “fatty acid.” The number of carbons in the fatty acid may range from 4 to 36; most common are those containing 12–18 carbons. In a fat molecule, the fatty acids are attached to each of the three carbons of the glycerol molecule with an ester bond through an oxygen atom ([\[link\]](#)).

Glycerol

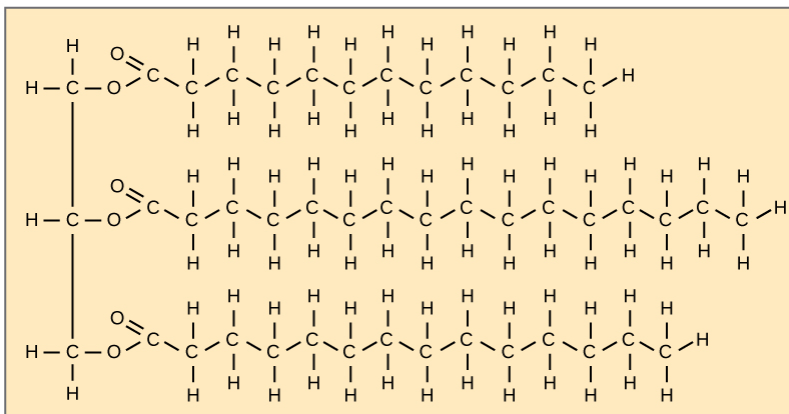


+

Fatty Acid



Triacylglycerol



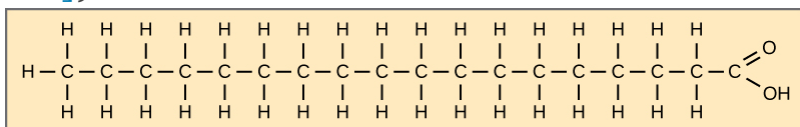
During this ester bond formation, three water molecules are released. The three fatty acids in the triacylglycerol may be similar or dissimilar. Fats are also called **triacylglycerols** or **triglycerides** because of their chemical structure. Some fatty acids have common names that specify their origin. For example, palmitic acid, a **saturated fatty acid**, is

derived from the palm tree. Arachidic acid is derived from *Arachis hypogea*, the scientific name for groundnuts or peanuts.

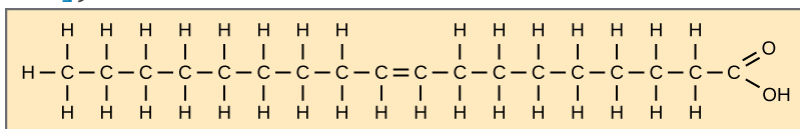
Fatty acids may be saturated or unsaturated. In a fatty acid chain, if there are only single bonds between neighboring carbons in the hydrocarbon chain, the fatty acid is said to be saturated.

Saturated fatty acids are saturated with hydrogen; in other words, the number of hydrogen atoms attached to the carbon skeleton is maximized.

Stearic acid is an example of a saturated fatty acid ([\[link\]](#))



When the hydrocarbon chain contains a double bond, the fatty acid is said to be **unsaturated**. Oleic acid is an example of an unsaturated fatty acid ([\[link\]](#)).

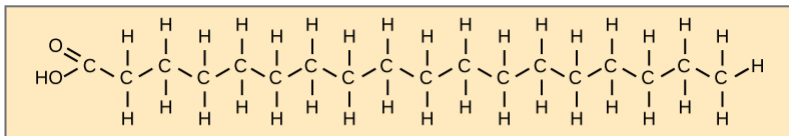


Most unsaturated fats are liquid at room temperature and are called oils. If there is one double bond in the molecule, then it is known as a monounsaturated fat (e.g., olive oil), and if there is more than one double bond, then it is known as a polyunsaturated fat (e.g., canola oil).

When a fatty acid has no double bonds, it is known as a saturated fatty acid because no more hydrogen may be added to the carbon atoms of the chain. A fat may contain similar or different fatty acids attached to glycerol. Long straight fatty acids with single bonds tend to get packed tightly and are solid at room temperature. Animal fats with stearic acid and palmitic acid (common in meat) and the fat with butyric acid (common in butter) are examples of saturated fats. Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the cell's volume. In plants, fat or oil is stored in many seeds and is used as a source of energy during seedling development. Unsaturated fats or oils are usually of plant origin and contain *cis* unsaturated fatty acids. *Cis* and *trans* indicate the configuration of the molecule around the double bond. If hydrogens are present in the same plane, it is referred to as a *cis* fat; if the hydrogen atoms are on two different planes, it is referred to as a **trans fat**. The *cis* double bond causes a bend or a “kink” that prevents the fatty acids from packing tightly, keeping them liquid at room temperature ([\[link\]](#)). Olive oil, corn oil, canola oil, and cod liver oil are examples of unsaturated fats. Unsaturated fats help to lower blood cholesterol levels whereas saturated fats contribute to plaque formation in the arteries.

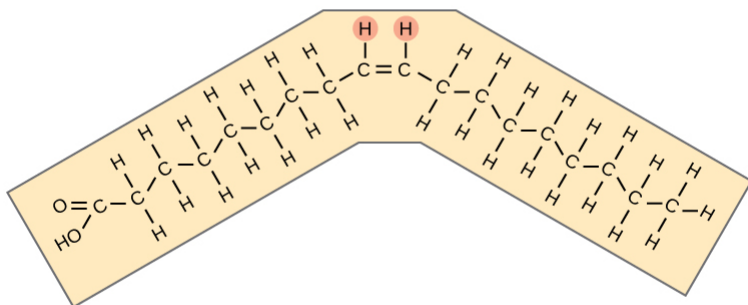
Saturated fatty acid

Stearic acid

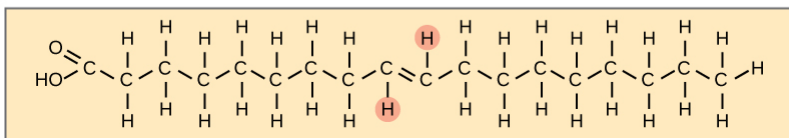


Unsaturated fatty acids

Cis oleic acid



Trans oleic acid



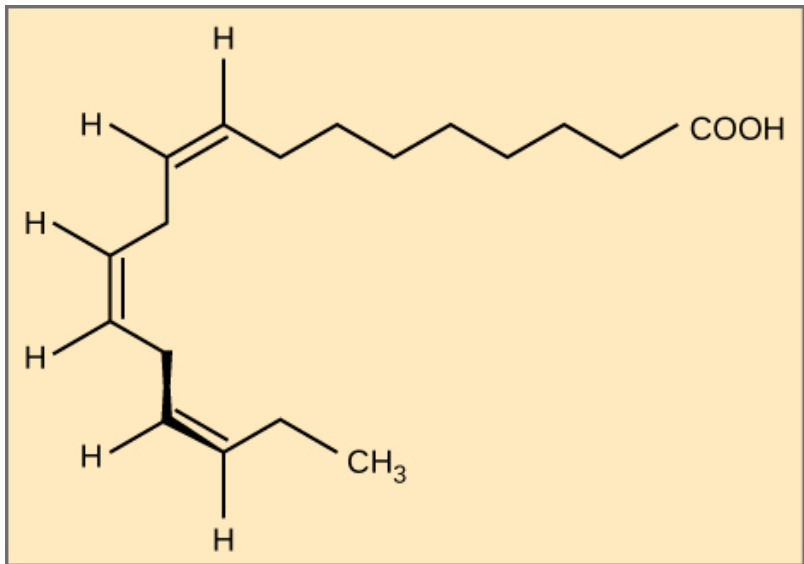
Trans Fats

In the food industry, oils are artificially hydrogenated to make them semi-solid and of a consistency desirable for many processed food products. Simply speaking, hydrogen gas is bubbled through oils to solidify them. During this hydrogenation process, double bonds of the *cis*-conformation in the hydrocarbon chain may be converted to double bonds in the *trans*-conformation.

Margarine, some types of peanut butter, and shortening are examples of artificially hydrogenated trans fats. Recent studies have shown that an increase in trans fats in the human diet may lead to an increase in levels of low-density lipoproteins (LDL), or “bad” cholesterol, which in turn may lead to plaque deposition in the arteries, resulting in heart disease. Many fast food restaurants have recently banned the use of trans fats, and food labels are required to display the trans fat content.

Omega Fatty Acids

Essential fatty acids are fatty acids required but not synthesized by the human body. Consequently, they have to be supplemented through ingestion via the diet. **Omega-3** fatty acids (like that shown in [\[link\]](#)) fall into this category and are one of only two known for humans (the other being omega-6 fatty acid). These are polyunsaturated fatty acids and are called omega-3 because the third carbon from the end of the hydrocarbon chain is connected to its neighboring carbon by a double bond.



The farthest carbon away from the carboxyl group is numbered as the omega (ω) carbon, and if the double bond is between the third and fourth carbon from that end, it is known as an omega-3 fatty acid. Nutritionally important because the body does not make them, omega-3 fatty acids include alpha-linolenic acid (ALA), eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA), all of which are polyunsaturated. Salmon, trout, and tuna are good sources of omega-3 fatty acids. Research indicates that omega-3 fatty acids reduce the risk of sudden death from heart attacks, reduce triglycerides in the blood, lower blood pressure, and prevent thrombosis by inhibiting blood clotting. They also reduce inflammation, and may help reduce the risk of some cancers in animals.

Like carbohydrates, fats have received a lot of bad

publicity. It is true that eating an excess of fried foods and other “fatty” foods leads to weight gain. However, fats do have important functions. Many vitamins are fat soluble, and fats serve as a long-term storage form of fatty acids: a source of energy. They also provide insulation for the body. Therefore, “healthy” fats in moderate amounts should be consumed on a regular basis. Waxy coverings on some leaves are made of lipids. (credit: Roger Griffith)

Waxes

Wax covers the feathers of some aquatic birds and the leaf surfaces of some plants. Because of the hydrophobic nature of waxes, they prevent water from sticking on the surface ([\[link\]](#)). Waxes are made up of long fatty acid chains esterified to long-chain alcohols.

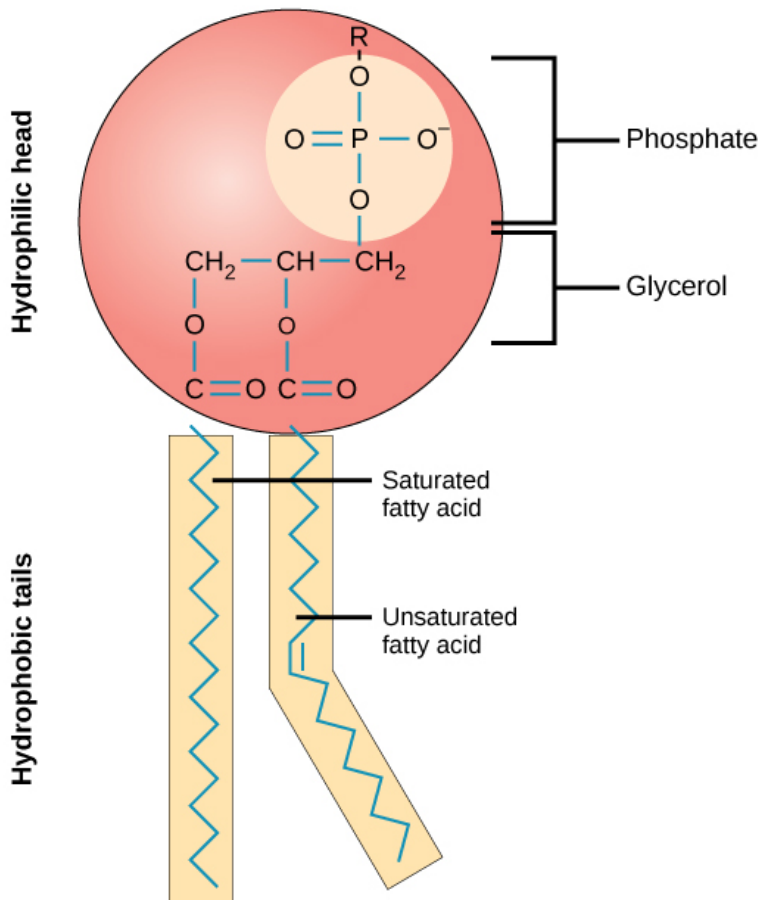


A phospholipid is a molecule with two fatty acids and a modified phosphate group attached to a glycerol backbone. The phosphate may be modified by the addition of charged or polar chemical groups. Two chemical groups that may modify the phosphate, choline and serine, are shown here. Both choline and serine attach to the phosphate group at the position labeled R via the hydroxyl group indicated in green. The phospholipid bilayer is the major component of all cellular membranes. The hydrophilic head groups of the phospholipids face the aqueous solution. The hydrophobic tails are sequestered in the middle of the bilayer.

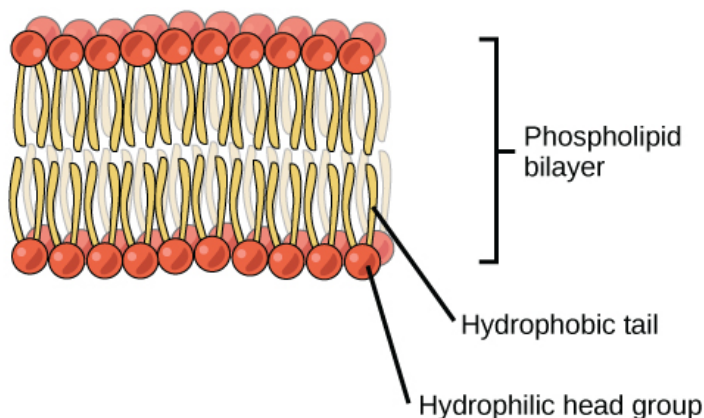
Phospholipids

Phospholipids are major constituents of the plasma

membrane, the outermost layer of animal cells. Like fats, they are composed of fatty acid chains attached to a glycerol or sphingosine backbone. Instead of three fatty acids attached as in triglycerides, however, there are two fatty acids forming diacylglycerol, and the third carbon of the glycerol backbone is occupied by a modified phosphate group ([\[link\]](#)). A phosphate group alone attached to a diacylglycerol does not qualify as a phospholipid; it is phosphatidate (diacylglycerol 3-phosphate), the precursor of phospholipids. The phosphate group is modified by an alcohol. Phosphatidylcholine and phosphatidylserine are two important phospholipids that are found in plasma membranes.



A phospholipid is an amphipathic molecule, meaning it has a hydrophobic and a hydrophilic part. The fatty acid chains are hydrophobic and cannot interact with water, whereas the phosphate-containing group is hydrophilic and interacts with water ([\[link\]](#)).



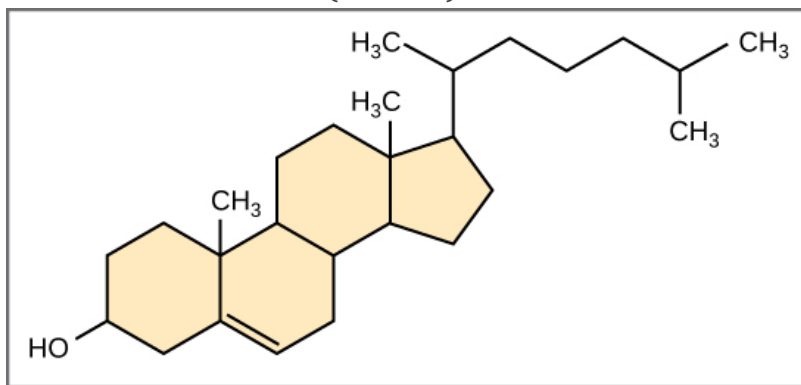
The head is the hydrophilic part, and the tail contains the hydrophobic fatty acids. In a membrane, a bilayer of phospholipids forms the matrix of the structure, the fatty acid tails of phospholipids face inside, away from water, whereas the phosphate group faces the outside, aqueous side ([\[link\]](#)).

Phospholipids are responsible for the dynamic nature of the plasma membrane. If a drop of phospholipids is placed in water, it spontaneously forms a structure known as a micelle, where the hydrophilic phosphate heads face the outside and the fatty acids face the interior of this structure. Steroids such as cholesterol and cortisol are composed of four fused hydrocarbon rings.

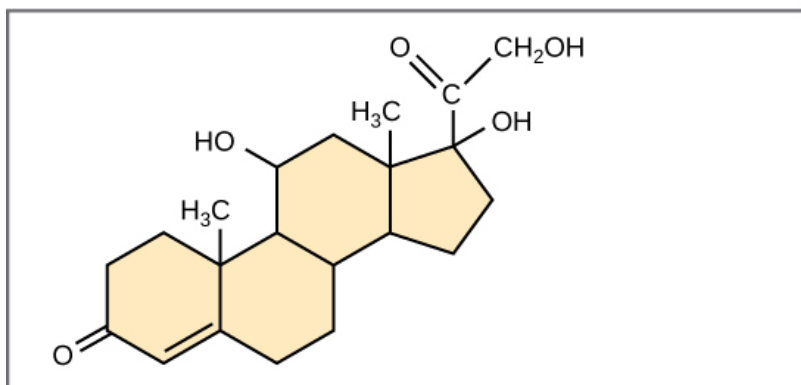
Steroids

Unlike the phospholipids and fats discussed earlier,

steroids have a fused ring structure. Although they do not resemble the other lipids, they are grouped with them because they are also hydrophobic and insoluble in water. All steroids have four linked carbon rings and several of them, like cholesterol, have a short tail ([\[link\]](#)). Many steroids also have the -OH functional group, which puts them in the alcohol classification (sterols).



Cholesterol



Cortisol

Cholesterol is the most common steroid. Cholesterol is mainly synthesized in the liver and is the

precursor to many steroid hormones such as testosterone and estradiol, which are secreted by the gonads and endocrine glands. It is also the precursor to Vitamin D. Cholesterol is also the precursor of bile salts, which help in the emulsification of fats and their subsequent absorption by cells. Although cholesterol is often spoken of in negative terms by lay people, it is necessary for proper functioning of the body. It is a component of the plasma membrane of animal cells and is found within the phospholipid bilayer. Being the outermost structure in animal cells, the plasma membrane is responsible for the transport of materials and cellular recognition and it is involved in cell-to-cell communication.

Link to Learning



For an additional perspective on lipids, explore the interactive animation “[Biomolecules: The Lipids](#)”

Section Summary

Lipids are a class of macromolecules that are nonpolar and hydrophobic in nature. Major types include fats and oils, waxes, phospholipids, and steroids. Fats are a stored form of energy and are also known as triacylglycerols or triglycerides. Fats are made up of fatty acids and either glycerol or sphingosine. Fatty acids may be unsaturated or saturated, depending on the presence or absence of double bonds in the hydrocarbon chain. If only single bonds are present, they are known as saturated fatty acids. Unsaturated fatty acids may have one or more double bonds in the hydrocarbon chain. Phospholipids make up the matrix of membranes. They have a glycerol or sphingosine backbone to which two fatty acid chains and a phosphate-containing group are attached. Steroids are another class of lipids. Their basic structure has four fused carbon rings. Cholesterol is a type of steroid and is an important constituent of the plasma membrane, where it helps to maintain the fluid nature of the membrane. It is also the precursor of steroid hormones such as testosterone.

Review Questions

Saturated fats have all of the following characteristics except:

1. they are solid at room temperature
2. they have single bonds within the carbon chain
3. they are usually obtained from animal sources
4. they tend to dissolve in water easily

D

Phospholipids are important components of _____.

1. the plasma membrane of animal cells
2. the ring structure of steroids
3. the waxy covering on leaves
4. the double bond in hydrocarbon chains

A

Free Response

Explain at least three functions that lipids serve

in plants and/or animals.

Fat serves as a valuable way for animals to store energy. It can also provide insulation. Waxes can protect plant leaves and mammalian fur from getting wet. Phospholipids and steroids are important components of animal cell membranes, as well as plant, fungal, and bacterial membranes.

Why have trans fats been banned from some restaurants? How are they created?

Trans fats are created artificially when hydrogen gas is bubbled through oils to solidify them. The double bonds of the *cis* conformation in the hydrocarbon chain may be converted to double bonds in the *trans* configuration. Some restaurants are banning trans fats because they cause higher levels of LDL, or “bad” cholesterol.

Glossary

lipid

macromolecule that is nonpolar and insoluble in water

omega fat

type of polyunsaturated fat that is required by the body; the numbering of the carbon omega starts from the methyl end or the end that is farthest from the carboxylic end

phospholipid

major constituent of the membranes; composed of two fatty acids and a phosphate-containing group attached to a glycerol backbone

saturated fatty acid

long-chain of hydrocarbon with single covalent bonds in the carbon chain; the number of hydrogen atoms attached to the carbon skeleton is maximized

steroid

type of lipid composed of four fused hydrocarbon rings forming a planar structure

trans fat

fat formed artificially by hydrogenating oils, leading to a different arrangement of double bond(s) than those found in naturally occurring lipids

triacylglycerol (also, triglyceride)

fat molecule; consists of three fatty acids linked to a glycerol molecule

unsaturated fatty acid

long-chain hydrocarbon that has one or more double bonds in the hydrocarbon chain

wax

lipid made of a long-chain fatty acid that is esterified to a long-chain alcohol; serves as a protective coating on some feathers, aquatic mammal fur, and leaves

Nucleic Acids

By the end of this section, you will be able to:

- Describe the structure of nucleic acids and define the two types of nucleic acids
- Explain the structure and role of DNA
- Explain the structure and roles of RNA

Nucleic acids are the most important macromolecules for the continuity of life. They carry the genetic blueprint of a cell and carry instructions for the functioning of the cell.

A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1' through 5' (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1' position of the ribose, and the phosphate is attached to the 5' position. When a polynucleotide is formed, the 5' phosphate of the incoming nucleotide attaches to the 3' hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA).

Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2' position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

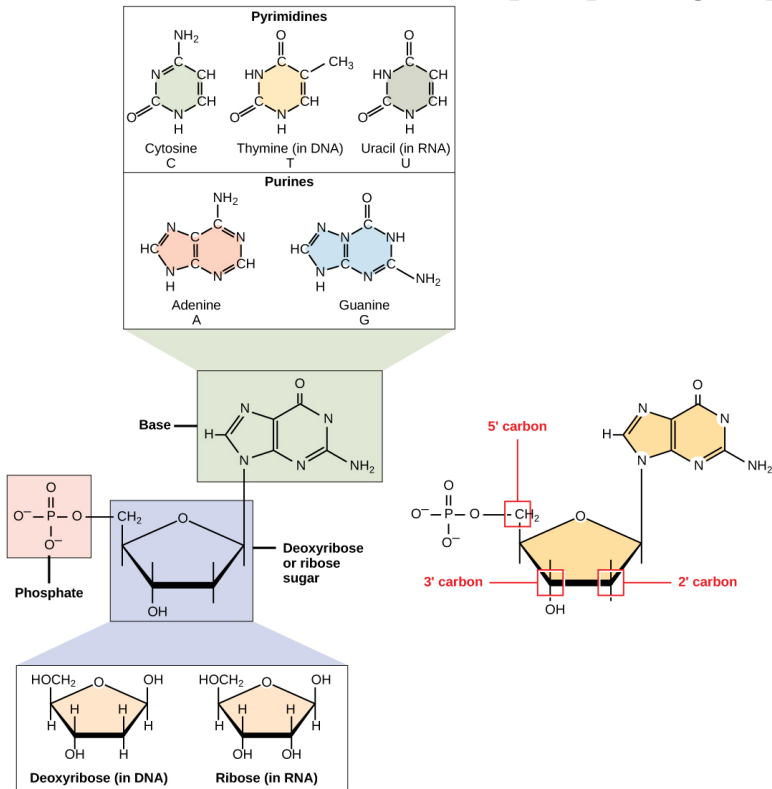
DNA and RNA

The two main types of nucleic acids are **deoxyribonucleic acid (DNA)** and **ribonucleic acid (RNA)**. DNA is the genetic material found in all living organisms, ranging from single-celled bacteria to multicellular mammals. It is found in the nucleus of eukaryotes and in the organelles, chloroplasts, and mitochondria. In prokaryotes, the DNA is not enclosed in a membranous envelope.

The entire genetic content of a cell is known as its genome, and the study of genomes is genomics. In eukaryotic cells but not in prokaryotes, DNA forms a complex with histone proteins to form chromatin, the substance of eukaryotic chromosomes. A chromosome may contain tens of thousands of genes. Many genes contain the information to make protein products; other genes code for RNA products. DNA controls all of the cellular activities by turning the genes “on” or “off.”

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. The DNA molecules never leave the nucleus but instead use an intermediary to communicate with the rest of the cell. This intermediary is the **messenger RNA (mRNA)**. Other types of RNA—like rRNA, tRNA, and microRNA—are involved in protein synthesis and its regulation.

DNA and RNA are made up of monomers known as **nucleotides**. The nucleotides combine with each other to form a **polynucleotide**, DNA or RNA. Each nucleotide is made up of three components: a nitrogenous base, a pentose (five-carbon) sugar, and a phosphate group ([\[link\]](#)). Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to one or more phosphate groups.



The nitrogenous bases, important components of nucleotides, are organic molecules and are so named because they contain carbon and nitrogen. They are bases because they contain an amino group that has the potential of binding an extra hydrogen, and

thus, decreases the hydrogen ion concentration in its environment, making it more basic. Each nucleotide in DNA contains one of four possible nitrogenous bases: adenine (A), guanine (G) cytosine (C), and thymine (T).

Adenine and guanine are classified as **purines**. The primary structure of a purine is two carbon-nitrogen rings. Cytosine, thymine, and uracil are classified as **pyrimidines** which have a single carbon-nitrogen ring as their primary structure ([\[link\]](#)). Each of these basic carbon-nitrogen rings has different functional groups attached to it. In molecular biology shorthand, the nitrogenous bases are simply known by their symbols A, T, G, C, and U. DNA contains A, T, G, and C whereas RNA contains A, U, G, and C.

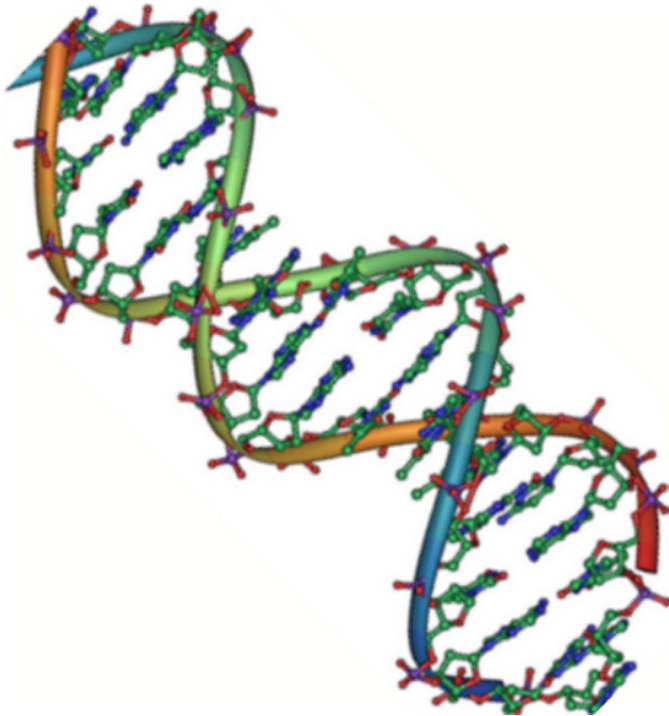
The pentose sugar in DNA is deoxyribose, and in RNA, the sugar is ribose ([\[link\]](#)). The difference between the sugars is the presence of the hydroxyl group on the second carbon of the ribose and hydrogen on the second carbon of the deoxyribose. The carbon atoms of the sugar molecule are numbered as 1', 2', 3', 4', and 5' (1' is read as "one prime"). The phosphate residue is attached to the hydroxyl group of the 5' carbon of one sugar and the hydroxyl group of the 3' carbon of the sugar of the next nucleotide, which forms a 5'-3' **phosphodiester** linkage. The phosphodiester linkage is not formed by simple dehydration

reaction like the other linkages connecting monomers in macromolecules: its formation involves the removal of two phosphate groups. A polynucleotide may have thousands of such phosphodiester linkages.

Native DNA is an antiparallel double helix. The phosphate backbone (indicated by the curvy lines) is on the outside, and the bases are on the inside. Each base from one strand interacts via hydrogen bonding with a base from the opposing strand.
(credit: Jerome Walker/Dennis Myts)

DNA Double-Helix Structure

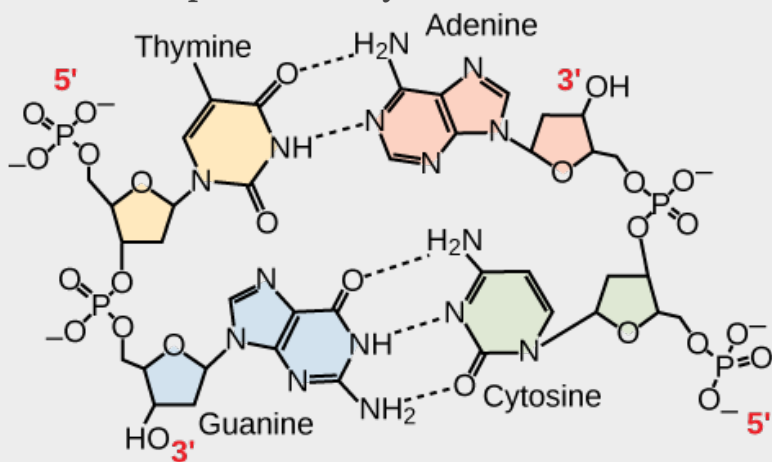
DNA has a double-helix structure ([\[link\]](#)). The sugar and phosphate lie on the outside of the helix, forming the backbone of the DNA. The nitrogenous bases are stacked in the interior, like the steps of a staircase, in pairs; the pairs are bound to each other by hydrogen bonds. Every base pair in the double helix is separated from the next base pair by 0.34 nm. The two strands of the helix run in opposite directions, meaning that the 5' carbon end of one strand will face the 3' carbon end of its matching strand. (This is referred to as antiparallel orientation and is important to DNA replication and in many nucleic acid interactions.)



Only certain types of base pairing are allowed. For example, a certain purine can only pair with a certain pyrimidine. This means A can pair with T, and G can pair with C, as shown in [\[link\]](#). This is known as the base complementary rule. In other words, the DNA strands are complementary to each other. If the sequence of one strand is AATTGGCC, the complementary strand would have the sequence TTAACCGG. During DNA replication, each strand is copied, resulting in a daughter DNA double helix containing one parental DNA strand and a newly synthesized strand.

Art Connection

In a double stranded DNA molecule, the two strands run antiparallel to one another so that one strand runs 5' to 3' and the other 3' to 5'. The phosphate backbone is located on the outside, and the bases are in the middle. Adenine forms hydrogen bonds (or base pairs) with thymine, and guanine base pairs with cytosine.



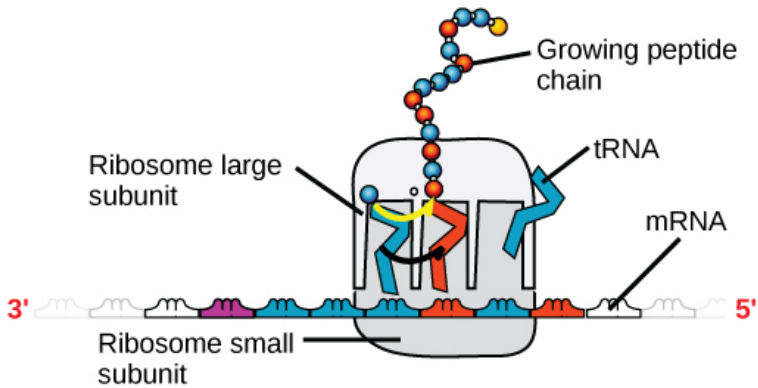
A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

A ribosome has two parts: a large subunit and a small subunit. The mRNA sits in between the two subunits. A tRNA molecule recognizes a codon on the mRNA, binds to it by complementary base pairing, and adds the correct amino acid to the growing peptide chain.

RNA

Ribonucleic acid, or RNA, is mainly involved in the process of protein synthesis under the direction of DNA. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester bonds. A ribonucleotide in the RNA chain contains ribose (the pentose sugar), one of the four nitrogenous bases (A, U, G, and C), and the phosphate group.

There are four major types of RNA: messenger RNA (mRNA), ribosomal RNA (rRNA), transfer RNA (tRNA), and microRNA (miRNA). The first, mRNA, carries the message from DNA, which controls all of the cellular activities in a cell. If a cell requires a certain protein to be synthesized, the gene for this product is turned “on” and the messenger RNA is synthesized in the nucleus. The RNA base sequence is complementary to the coding sequence of the DNA from which it has been copied. However, in RNA, the base T is absent and U is present instead. If the DNA strand has a sequence AATTGCGC, the sequence of the complementary RNA is UUAACGCG. In the cytoplasm, the mRNA interacts with ribosomes and other cellular machinery ([\[link\]](#)).



The mRNA is read in sets of three bases known as codons. Each codon codes for a single amino acid. In this way, the mRNA is read and the protein product is made. **Ribosomal RNA (rRNA)** is a major constituent of ribosomes on which the mRNA binds. The rRNA ensures the proper alignment of the mRNA and the ribosomes; the rRNA of the ribosome also has an enzymatic activity (peptidyl transferase) and catalyzes the formation of the peptide bonds between two aligned amino acids. **Transfer RNA (tRNA)** is one of the smallest of the four types of RNA, usually 70–90 nucleotides long. It carries the correct amino acid to the site of protein synthesis. It is the base pairing between the tRNA and mRNA that allows for the correct amino acid to be inserted in the polypeptide chain. microRNAs are the smallest RNA molecules and their role involves the regulation of gene expression by interfering with the expression of certain mRNA messages. [\[link\]](#) summarizes features of DNA and RNA.

Features of DNA and RNA		
	DNA	RNA
Function	Carries genetic information	Involved in protein synthesis
Location	Remains in the nucleus	Leaves the nucleus
Structure	Double helix	Usually single-stranded
Sugar	Deoxyribose	Ribose
Pyrimidines	Cytosine, thymine	Cytosine, uracil
Purines	Adenine, guanine	Adenine, guanine

Even though the RNA is single stranded, most RNA types show extensive intramolecular base pairing between complementary sequences, creating a predictable three-dimensional structure essential for their function.

As you have learned, information flow in an organism takes place from DNA to RNA to protein. DNA dictates the structure of mRNA in a process known as **transcription**, and RNA dictates the structure of protein in a process known as **translation**. This is known as the Central Dogma of Life, which holds true for all organisms; however, exceptions to the rule occur in connection with viral infections.

Link to Learning



To learn more about DNA, explore the [Howard Hughes Medical Institute BioInteractive animations](#) on the topic of DNA.

Section Summary

Nucleic acids are molecules made up of nucleotides that direct cellular activities such as cell division and protein synthesis. Each nucleotide is made up of a pentose sugar, a nitrogenous base, and a phosphate group. There are two types of nucleic acids: DNA and RNA. DNA carries the genetic blueprint of the cell and is passed on from parents to offspring (in the form of chromosomes). It has a double-helical structure with the two strands running in opposite directions, connected by hydrogen bonds, and complementary to each other.

RNA is single-stranded and is made of a pentose sugar (ribose), a nitrogenous base, and a phosphate group. RNA is involved in protein synthesis and its regulation. Messenger RNA (mRNA) is copied from the DNA, is exported from the nucleus to the cytoplasm, and contains information for the construction of proteins. Ribosomal RNA (rRNA) is a part of the ribosomes at the site of protein synthesis, whereas transfer RNA (tRNA) carries the amino acid to the site of protein synthesis. microRNA regulates the use of mRNA for protein synthesis.

Art Connections

[\[link\]](#) A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

[\[link\]](#) Adenine is larger than cytosine and will not be able to base pair properly with the guanine on the opposing strand. This will cause the DNA to bulge. DNA repair enzymes may recognize the bulge and replace the incorrect nucleotide.

Review Questions

A nucleotide of DNA may contain _____.

1. ribose, uracil, and a phosphate group
 2. deoxyribose, uracil, and a phosphate group
 3. deoxyribose, thymine, and a phosphate group
 4. ribose, thymine, and a phosphate group
-

C

The building blocks of nucleic acids are _____.

1. sugars
 2. nitrogenous bases
 3. peptides
 4. nucleotides
-

D

Free Response

What are the structural differences between

RNA and DNA?

DNA has a double-helix structure. The sugar and the phosphate are on the outside of the helix and the nitrogenous bases are in the interior. The monomers of DNA are nucleotides containing deoxyribose, one of the four nitrogenous bases (A, T, G and C), and a phosphate group. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester linkages. A ribonucleotide contains ribose (the pentose sugar), one of the four nitrogenous bases (A, U, G, and C), and the phosphate group.

What are the four types of RNA and how do they function?

The four types of RNA are messenger RNA, ribosomal RNA, transfer RNA, and microRNA. Messenger RNA carries the information from the DNA that controls all cellular activities. The mRNA binds to the ribosomes that are constructed of proteins and rRNA, and tRNA transfers the correct amino acid to the site of protein synthesis. microRNA regulates the availability of mRNA for translation.

Glossary

deoxyribonucleic acid (DNA)

double-helical molecule that carries the hereditary information of the cell

messenger RNA (mRNA)

RNA that carries information from DNA to ribosomes during protein synthesis

nucleic acid

biological macromolecule that carries the genetic blueprint of a cell and carries instructions for the functioning of the cell

nucleotide

monomer of nucleic acids; contains a pentose sugar, one or more phosphate groups, and a nitrogenous base

phosphodiester

linkage covalent chemical bond that holds together the polynucleotide chains with a phosphate group linking two pentose sugars of neighboring nucleotides

polynucleotide

long chain of nucleotides

purine

type of nitrogenous base in DNA and RNA; adenine and guanine are purines

pyrimidine

type of nitrogenous base in DNA and RNA;
cytosine, thymine, and uracil are pyrimidines

ribonucleic acid (RNA)

single-stranded, often internally base paired,
molecule that is involved in protein synthesis

ribosomal RNA (rRNA)

RNA that ensures the proper alignment of the
mRNA and the ribosomes during protein
synthesis and catalyzes the formation of the
peptide linkage

transcription

process through which messenger RNA forms
on a template of DNA

transfer RNA (tRNA)

RNA that carries activated amino acids to the
site of protein synthesis on the ribosome

translation

process through which RNA directs the
formation of protein

Studying Cells

By the end of this section, you will be able to:

- Describe the role of cells in organisms
- Compare and contrast light microscopy and electron microscopy
- Summarize cell theory

A cell is the smallest unit of a living thing. A living thing, whether made of one cell (like bacteria) or many cells (like a human), is called an organism. Thus, cells are the basic building blocks of all organisms.

Several cells of one kind that interconnect with each other and perform a shared function form tissues, several tissues combine to form an organ (your stomach, heart, or brain), and several organs make up an organ system (such as the digestive system, circulatory system, or nervous system). Several systems that function together form an organism (like a human being). Here, we will examine the structure and function of cells.

There are many types of cells, all grouped into one of two broad categories: prokaryotic and eukaryotic. For example, both animal and plant cells are classified as eukaryotic cells, whereas bacterial cells are classified as prokaryotic. Before discussing the criteria for determining whether a cell is prokaryotic or eukaryotic, let's first examine how biologists

study cells.

(a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times and have a resolution of about 200 nanometers. (b) Electron microscopes provide a much higher magnification, 100,000x, and have a resolution of 50 picometers. (credit a: modification of work by "GcG"/Wikimedia Commons; credit b: modification of work by Evan Bench) (a) These *Salmonella* bacteria appear as tiny purple dots when viewed with a light microscope. (b) This scanning electron microscope micrograph shows *Salmonella* bacteria (in red) invading human cells (yellow). Even though subfigure (b) shows a different *Salmonella* specimen than subfigure (a), you can still observe the comparative increase in magnification and detail. (credit a: modification of work by CDC/Armed Forces Institute of Pathology, Charles N. Farmer, Rocky Mountain Laboratories; credit b: modification of work by NIAID, NIH; scale-bar data from Matt Russell)

Microscopy

Cells vary in size. With few exceptions, individual cells cannot be seen with the naked eye, so scientists use microscopes (micro- = “small”; -scope = “to look at”) to study them. A **microscope** is an instrument that magnifies an object. Most photographs of cells are taken with a microscope, and these images can also be called micrographs.

The optics of a microscope's lenses change the orientation of the image that the user sees. A specimen that is right-side up and facing right on the microscope slide will appear upside-down and facing left when viewed through a microscope, and vice versa. Similarly, if the slide is moved left while looking through the microscope, it will appear to move right, and if moved down, it will seem to move up. This occurs because microscopes use two sets of lenses to magnify the image. Because of the manner by which light travels through the lenses, this system of two lenses produces an inverted image (binocular, or dissecting microscopes, work in a similar manner, but include an additional magnification system that makes the final image appear to be upright).

Light Microscopes

To give you a sense of cell size, a typical human red blood cell is about eight millionths of a meter or eight micrometers (abbreviated as eight μm) in diameter; the head of a pin is about two thousandths of a meter (two mm) in diameter. That means about 250 red blood cells could fit on the head of a pin.

Most student microscopes are classified as **light microscopes** ([link](#)). Visible light passes and is bent through the lens system to enable the user to see the specimen. Light microscopes are

advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.

Light microscopes commonly used in the undergraduate college laboratory magnify up to approximately 400 times. Two parameters that are important in microscopy are magnification and resolving power. Magnification is the process of enlarging an object in appearance. Resolving power is the ability of a microscope to distinguish two adjacent structures as separate: the higher the resolution, the better the clarity and detail of the image. When oil immersion lenses are used for the study of small objects, magnification is usually increased to 1,000 times. In order to gain a better understanding of cellular structure and function, scientists typically use electron microscopes.



(a)



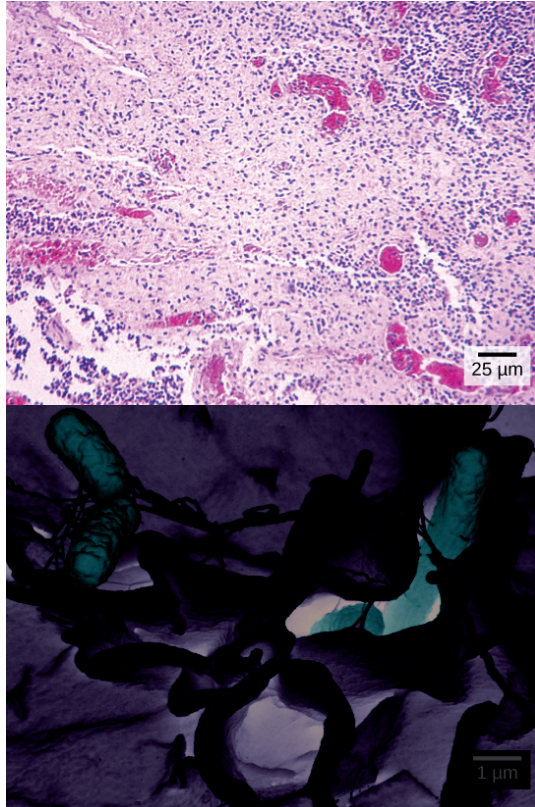
(b)

Electron Microscopes

In contrast to light microscopes, **electron microscopes** ([link](#)**b**) use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail ([link](#)), it also provides higher resolving power. The method used to prepare the specimen for viewing with an electron microscope kills the specimen. Electrons have short wavelengths (shorter than photons) that move best in a vacuum, so living cells cannot be viewed with an electron microscope.

In a scanning electron microscope, a beam of electrons moves back and forth across a cell's

surface, creating details of cell surface characteristics. In a transmission electron microscope, the electron beam penetrates the cell and provides details of a cell's internal structures. As you might imagine, electron microscopes are significantly more bulky and expensive than light microscopes.



Link to Learning



For another perspective on cell size, try the HowBig interactive at [this site](#).

Cell Theory

The microscopes we use today are far more complex than those used in the 1600s by Antony van Leeuwenhoek, a Dutch shopkeeper who had great skill in crafting lenses. Despite the limitations of his now-ancient lenses, van Leeuwenhoek observed the movements of protista (a type of single-celled organism) and sperm, which he collectively termed “animalcules.”

In a 1665 publication called *Micrographia*, experimental scientist Robert Hooke coined the term “cell” for the box-like structures he observed when viewing cork tissue through a lens. In the 1670s, van Leeuwenhoek discovered bacteria and protozoa. Later advances in lenses, microscope construction,

and staining techniques enabled other scientists to see some components inside cells.

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed the **unified cell theory**, which states that all living things are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells. Rudolf Virchow later made important contributions to this theory.

Career Connection

Cytotechnologist

Have you ever heard of a medical test called a Pap smear ([\[link\]](#))? In this test, a doctor takes a small sample of cells from the uterine cervix of a patient and sends it to a medical lab where a cytotechnologist stains the cells and examines them for any changes that could indicate cervical cancer or a microbial infection.

Cytotechnologists (cyto- = “cell”) are professionals who study cells via microscopic examinations and other laboratory tests. They are trained to determine which cellular changes are within normal limits and which are abnormal. Their focus is not limited to cervical cells; they study cellular specimens that come from all organs. When they notice abnormalities, they consult a pathologist, who is a medical doctor who can make a clinical

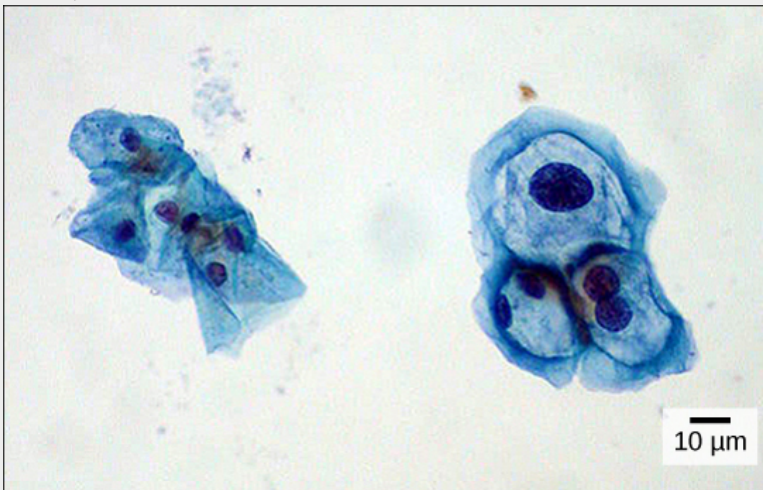
diagnosis.

Cytotechnologists play a vital role in saving people's lives. When abnormalities are discovered early, a patient's treatment can begin sooner, which usually increases the chances of a successful outcome.

These uterine cervix cells, viewed through a light microscope, were obtained from a Pap smear.

Normal cells are on the left. The cells on the right are infected with human papillomavirus (HPV).

Notice that the infected cells are larger; also, two of these cells each have two nuclei instead of one, the normal number. (credit: modification of work by Ed Uthman, MD; scale-bar data from Matt Russell)



Section Summary

A cell is the smallest unit of life. Most cells are so tiny that they cannot be seen with the naked eye. Therefore, scientists use microscopes to study cells. Electron microscopes provide higher magnification, higher resolution, and more detail than light microscopes. The unified cell theory states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells.

Review Questions

When viewing a specimen through a light microscope, scientists use _____ to distinguish the individual components of cells.

1. a beam of electrons
2. radioactive isotopes
3. special stains
4. high temperatures

C

The _____ is the basic unit of life.

1. organism
 2. cell
 3. tissue
 4. organ
-

B

Free Response

In your everyday life, you have probably noticed that certain instruments are ideal for certain situations. For example, you would use a spoon rather than a fork to eat soup because a spoon is shaped for scooping, while soup would slip between the tines of a fork. The use of ideal instruments also applies in science. In what situation(s) would the use of a light microscope be ideal, and why?

A light microscope would be ideal when viewing a small living organism, especially when the cell has been stained to reveal details.

In what situation(s) would the use of a scanning electron microscope be ideal, and why?

A scanning electron microscope would be ideal when you want to view the minute details of a cell's surface, because its beam of electrons moves back and forth over the surface to convey the image.

In what situation(s) would a transmission electron microscope be ideal, and why?

A transmission electron microscope would be ideal for viewing the cell's internal structures, because many of the internal structures have membranes that are not visible by the light microscope.

What are the advantages and disadvantages of each of these types of microscopes?

The advantages of light microscopes are that they are easily obtained, and the light beam does not kill the cells. However, typical light microscopes are somewhat limited in the amount of detail they can reveal. Electron microscopes are ideal because you can view intricate details, but they are bulky and costly, and preparation for the microscopic examination kills the specimen.

Glossary

cell theory

see unified cell theory

electron microscope

an instrument that magnifies an object using a beam of electrons passed and bent through a lens system to visualize a specimen

light microscope

an instrument that magnifies an object using a beam visible light passed and bent through a lens system to visualize a specimen

microscope

an instrument that magnifies an object

unified cell theory

a biological concept that states that all organisms are composed of one or more cells; the cell is the basic unit of life; and new cells arise from existing cells

Comparing Prokaryotic and Eukaryotic Cells

By the end of this section, you will be able to:

- Name examples of prokaryotic and eukaryotic organisms
- Compare and contrast prokaryotic cells and eukaryotic cells
- Describe the relative sizes of different kinds of cells

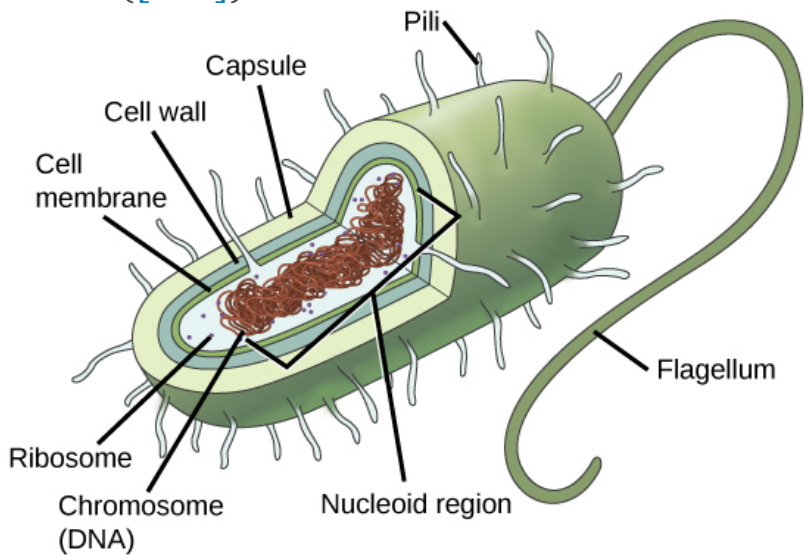
Cells fall into one of two broad categories: prokaryotic and eukaryotic. The predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (*pro-* = before; *-karyon-* = nucleus). Animal cells, plant cells, fungi, and protists are eukaryotes (*eu-* = true).

This figure shows the generalized structure of a prokaryotic cell.

Components of Prokaryotic Cells

All cells share four common components: 1) a plasma membrane, an outer covering that separates the cell's interior from its surrounding environment; 2) cytoplasm, consisting of a jelly-like region within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, particles that synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A **prokaryotic cell** is a simple, single-celled (unicellular) organism that lacks a nucleus, or any other membrane-bound organelle. We will shortly come to see that this is significantly different in eukaryotes. Prokaryotic DNA is found in the central part of the cell: a darkened region called the nucleoid ([\[link\]](#)).



Unlike Archaea and eukaryotes, bacteria have a cell wall made of peptidoglycan, comprised of sugars and amino acids, and many have a polysaccharide capsule ([\[link\]](#)). The cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents dehydration. The capsule enables the cell to attach to surfaces in its environment. Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion, while most pili are used to exchange genetic material during a type of reproduction called conjugation.

Eukaryotic Cells

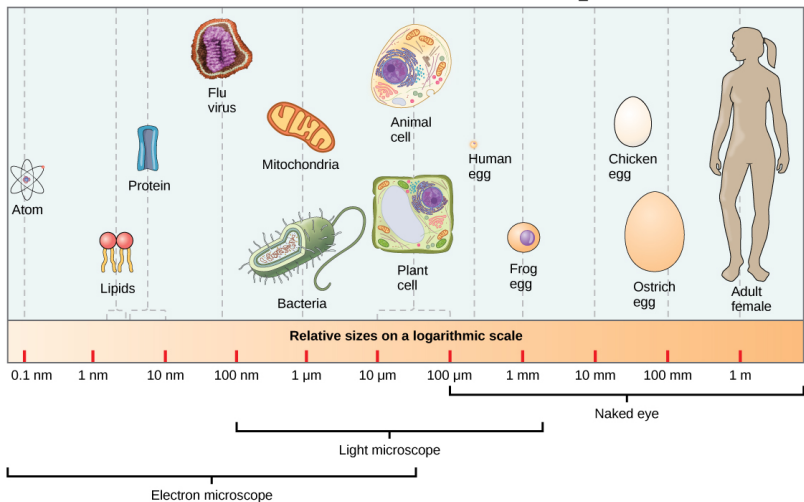
In nature, the relationship between form and function is apparent at all levels, including the level of the cell, and this will become clear as we explore eukaryotic cells. The principle “form follows function” is found in many contexts. For example, birds and fish have streamlined bodies that allow them to move quickly through the medium in which they live, be it air or water. It means that, in general, one can deduce the function of a structure by looking at its form, because the two are matched.

A **eukaryotic cell** is a cell that has a membrane-bound nucleus and other membrane-bound compartments or sacs, called **organelles**, which have specialized functions. The word eukaryotic means “true kernel” or “true nucleus,” alluding to the presence of the membrane-bound nucleus in these cells. The word “organelle” means “little organ,” and, as already mentioned, organelles have specialized cellular functions, just as the organs of your body have specialized functions.

This figure shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison.

Cell Size

At 0.1–5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10–100 μm ([link]). The small size of prokaryotes allows ions and organic molecules that enter them to quickly spread to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly move out. However, larger eukaryotic cells have evolved different structural adaptations to enhance cellular transport. Indeed, the large size of these cells would not be possible without these adaptations. In general, cell size is limited because volume increases much more quickly than does cell surface area. As a cell becomes larger, it becomes more and more difficult for the cell to acquire sufficient materials to support the processes inside the cell, because the relative size of the surface area across which materials must be transported declines.



Section Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, DNA, and lack membrane-bound organelles. Many also have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1–5.0 μm .

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. Eukaryotic cells tend to be 10 to 100 times the size of prokaryotic cells.

Multiple Choice

Which of these do all prokaryotes and eukaryotes share?

1. nuclear envelope
2. cell walls
3. organelles

4. plasma membrane

D

A typical prokaryotic cell _____
compared to a eukaryotic cell.

1. is smaller in size by a factor of 100
 2. is similar in size
 3. is smaller in size by a factor of one million
 4. is larger in size by a factor of 10
-

A

Free Response

Describe the structures that are characteristic of a prokaryote cell.

Prokaryotic cells are surrounded by a plasma membrane and have DNA, cytoplasm, and ribosomes, like eukaryotic cells. They also have cell walls and may have a cell capsule.

Prokaryotes have a single large chromosome that is not surrounded by a nuclear membrane.

Prokaryotes may have flagella or motility, pili for conjugation, and fimbriae for adhesion to surfaces.

Glossary

eukaryotic cell

a cell that has a membrane-bound nucleus and several other membrane-bound compartments or sacs

organelle

a membrane-bound compartment or sac within a cell

prokaryotic cell

a unicellular organism that lacks a nucleus or any other membrane-bound organelle

Prokaryotic Cells

By the end of this section, you will be able to:

- Name examples of prokaryotic and eukaryotic organisms
- Compare and contrast prokaryotic cells and eukaryotic cells
- Describe the relative sizes of different kinds of cells
- Explain why cells must be small

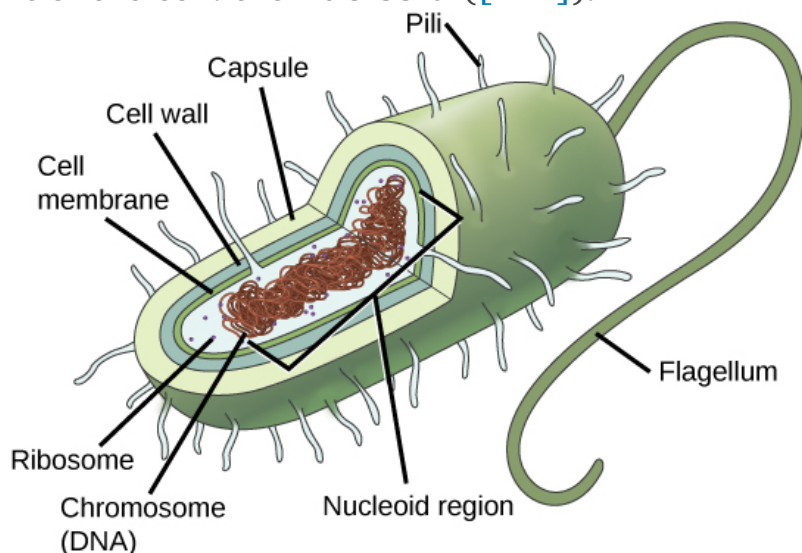
Cells fall into one of two broad categories: prokaryotic and eukaryotic. Only the predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (pro- = “before”; -kary- = “nucleus”). Animals, plants, fungi, and protists are all eukaryotes (eu- = “true”) and are made up of eukaryotic cells.

This figure shows the generalized structure of a prokaryotic cell. All prokaryotes have chromosomal DNA localized in a nucleoid, ribosomes, a cell membrane, and a cell wall. The other structures shown are present in some, but not all, bacteria. This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

Components of Prokaryotic Cells

All cells share four common components: 1) a plasma membrane, an outer covering that separates the cell's interior from its surrounding environment; 2) cytoplasm, consisting of a jelly-like cytosol within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, which synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A **prokaryote** is a simple, mostly single-celled (unicellular) organism that lacks a nucleus, or any other membrane-bound organelle. We will shortly come to see that this is significantly different in eukaryotes. Prokaryotic DNA is found in a central part of the cell: the **nucleoid** ([\[link\]](#)).



Most prokaryotes have a peptidoglycan cell wall and many have a polysaccharide capsule ([\[link\]](#)). The

cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents dehydration. The capsule enables the cell to attach to surfaces in its environment. Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion. Pili are used to exchange genetic material during a type of reproduction called conjugation. Fimbriae are used by bacteria to attach to a host cell.

Career Connection

Microbiologist

The most effective action anyone can take to prevent the spread of contagious illnesses is to wash his or her hands. Why? Because microbes (organisms so tiny that they can only be seen with microscopes) are ubiquitous. They live on doorknobs, money, your hands, and many other surfaces. If someone sneezes into his hand and touches a doorknob, and afterwards you touch that same doorknob, the microbes from the sneezer's mucus are now on your hands. If you touch your hands to your mouth, nose, or eyes, those microbes can enter your body and could make you sick. However, not all microbes (also called microorganisms) cause disease; most are actually beneficial. You have microbes in your gut that make vitamin K. Other microorganisms are used to ferment beer and wine.

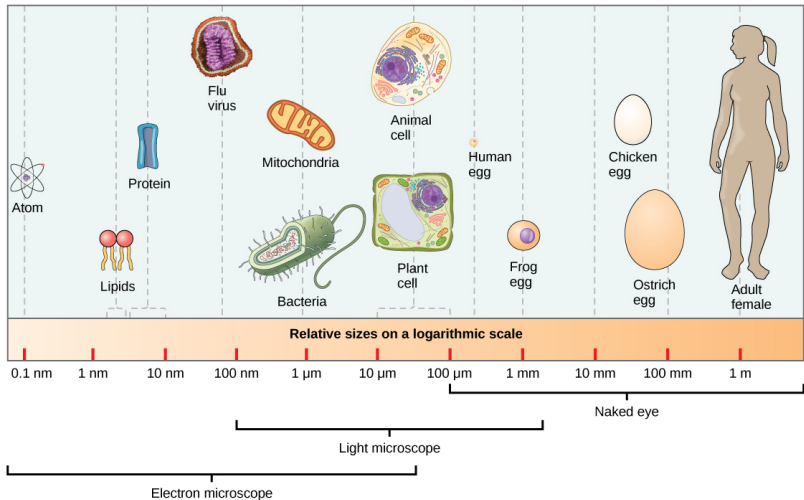
Microbiologists are scientists who study microbes. Microbiologists can pursue a number of careers. Not only do they work in the food industry, they are also employed in the veterinary and medical fields. They can work in the pharmaceutical sector, serving key roles in research and development by identifying new sources of antibiotics that could be used to treat bacterial infections.

Environmental microbiologists may look for new ways to use specially selected or genetically engineered microbes for the removal of pollutants from soil or groundwater, as well as hazardous elements from contaminated sites. These uses of microbes are called bioremediation technologies. Microbiologists can also work in the field of bioinformatics, providing specialized knowledge and insight for the design, development, and specificity of computer models of, for example, bacterial epidemics.

Cell Size

At 0.1 to 5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 μm ([\[link\]](#)). The small size of prokaryotes allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly

diffuse out. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

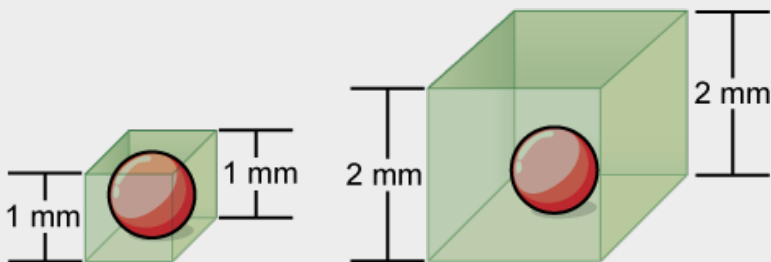


Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $\frac{4\pi r^3}{3}$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had the shape of a cube ([\[link\]](#)). If the cell grows too large, the plasma membrane will not have sufficient surface area to

support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide; another way is to develop organelles that perform specific tasks. These adaptations lead to the development of more sophisticated cells called eukaryotic cells.

Art Connection

Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of 1 mm^3 and a surface area of 6 mm^2 , with a surface area-to-volume ratio of 6 to 1, whereas the cell on the right has a volume of 8 mm^3 and a surface area of 24 mm^2 , with a surface area-to-volume ratio of 3 to 1.



Prokaryotic cells are much smaller than eukaryotic cells. What advantages might small cell size confer on a cell? What advantages might large cell size have?

Section Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, and DNA that is not membrane-bound. Most have peptidoglycan cell walls and many have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1 to 5.0 μm .

As a cell increases in size, its surface area-to-volume ratio decreases. If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume.

Art Connections

[\[link\]](#) Prokaryotic cells are much smaller than eukaryotic cells. What advantages might small cell size confer on a cell? What advantages might large cell size have?

[\[link\]](#) Substances can diffuse more quickly through small cells. Small cells have no need

for organelles and therefore do not need to expend energy getting substances across organelle membranes. Large cells have organelles that can separate cellular processes, enabling them to build molecules that are more complex.

Review Questions

Prokaryotes depend on _____ to obtain some materials and to get rid of wastes.

1. ribosomes
2. flagella
3. cell division
4. diffusion

D

Bacteria that lack fimbriae are less likely to _____.

1. adhere to cell surfaces
2. swim through bodily fluids
3. synthesize proteins
4. retain the ability to divide

Free Response

Antibiotics are medicines that are used to fight bacterial infections. These medicines kill prokaryotic cells without harming human cells. What part or parts of the bacterial cell do you think antibiotics target? Why?

The cell wall would be targeted by antibiotics as well as the bacteria's ability to replicate. This would inhibit the bacteria's ability to reproduce, and it would compromise its defense mechanisms.

Explain why not all microbes are harmful.

Some microbes are beneficial. For instance, *E. coli* bacteria populate the human gut and help break down fiber in the diet. Some foods such as yogurt are formed by bacteria.

Glossary

nucleoid

central part of a prokaryotic cell in which the chromosome is found

prokaryote

unicellular organism that lacks a nucleus or any other membrane-bound organelle

Eukaryotic Cells

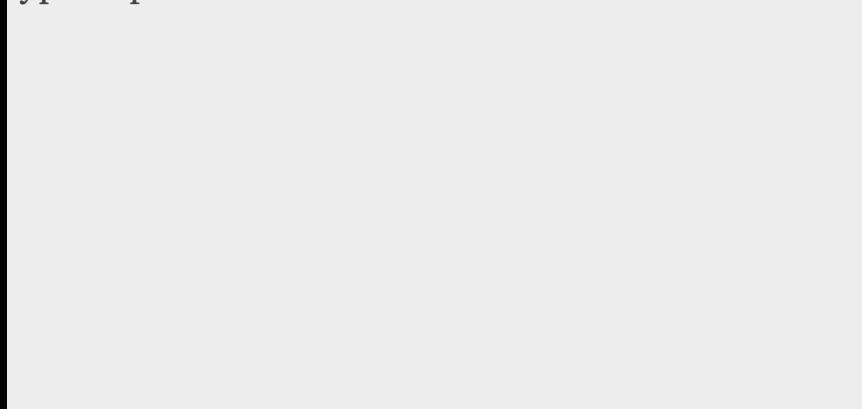
By the end of this section, you will be able to:

- Describe the structure of eukaryotic plant and animal cells
- State the role of the plasma membrane
- Summarize the functions of the major cell organelles
- Describe the cytoskeleton and extracellular matrix

At this point, it should be clear that eukaryotic cells have a more complex structure than do prokaryotic cells. Organelles allow for various functions to occur in the cell at the same time. Before discussing the functions of organelles within a eukaryotic cell, let us first examine two important components of the cell: the plasma membrane and the cytoplasm.

Art Connection

This figure shows (a) a typical animal cell and (b) a typical plant cell.



Nucleus

Nuclear envelope:

membrane enclosing the nucleus. Protein-lined pores allow material to move in and out.

Chromatin: DNA plus associated proteins.

Nucleolus:

condensed region where ribosomes are formed.

Cytoskeleton

Microtubules: form the mitotic spindle and maintain cell shape.

Centrosome: microtubule-organizing center.

Intermediate filaments: fibrous proteins that hold organelles in place.

Microfilaments:

fibrous proteins; form the cellular cortex.

Peroxisome:

metabolizes waste

Endoplasmic reticulum

Rough: associated with ribosomes; makes secretory and membrane proteins.

Smooth: makes lipids.

Plasma membrane

Lysosome:

digests food and waste materials.

Golgi apparatus: modifies proteins.

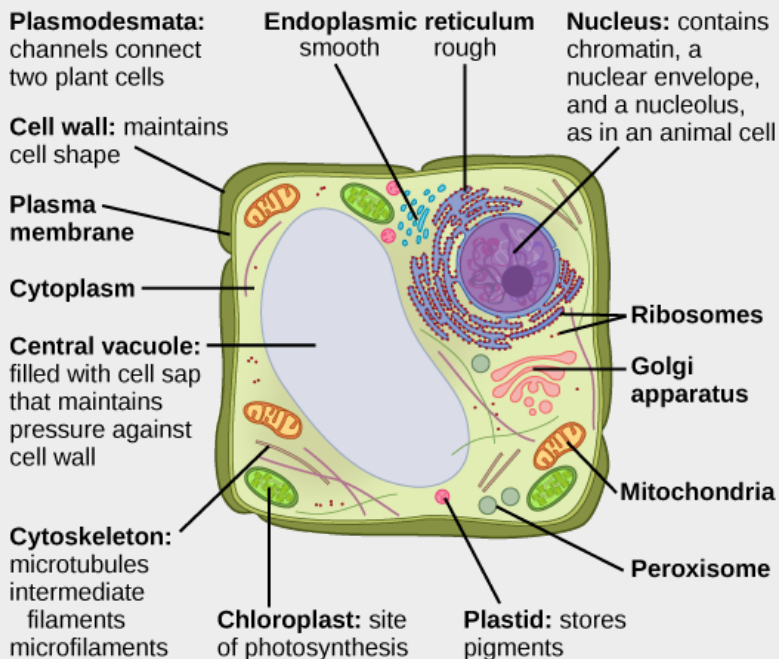
Cytoplasm

Mitochondria:

produce energy.

Vacuole

(a)



(b)

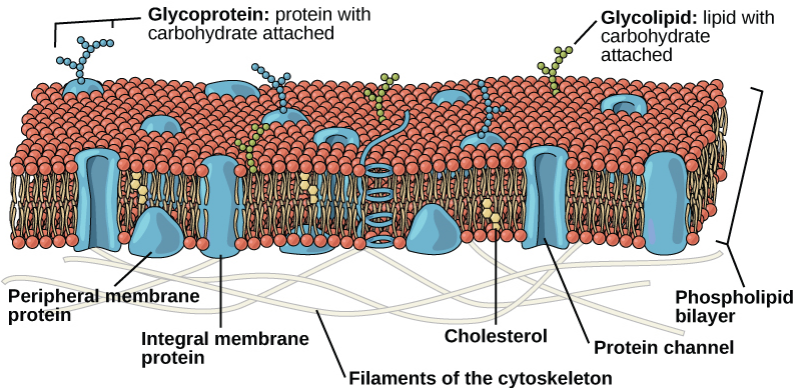
What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and carbohydrates, which can be found in the membrane in addition to phospholipids and protein.

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a **plasma**

membrane ([\[link\]](#)) made up of a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule composed of two fatty acid chains, a glycerol backbone, and a phosphate group. The plasma membrane regulates the passage of some substances, such as organic molecules, ions, and water, preventing the passage of some to maintain internal conditions, while actively bringing in or removing others. Other compounds move passively across the membrane.



The plasma membranes of cells that specialize in absorption are folded into fingerlike projections called microvilli (singular = microvillus). This folding increases the surface area of the plasma membrane. Such cells are typically found lining the small intestine, the organ that absorbs nutrients from digested food. This is an excellent example of form matching the function of a structure.

People with celiac disease have an immune response

to gluten, which is a protein found in wheat, barley, and rye. The immune response damages microvilli, and thus, afflicted individuals cannot absorb nutrients. This leads to malnutrition, cramping, and diarrhea. Patients suffering from celiac disease must follow a gluten-free diet.

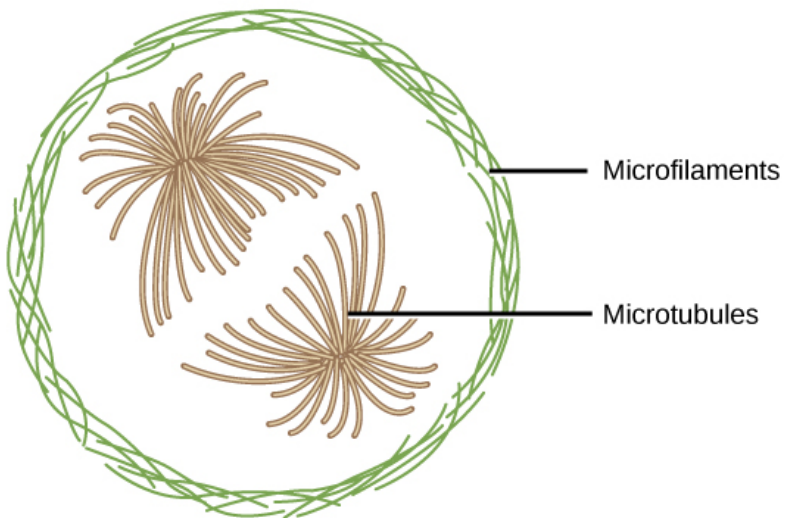
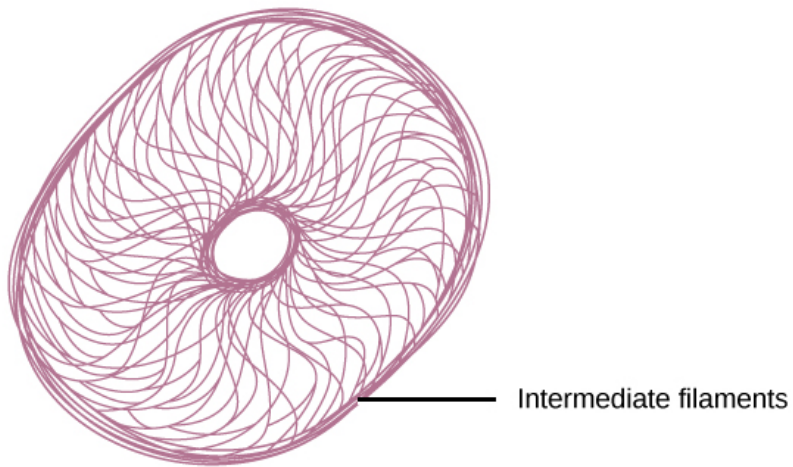
The Cytoplasm

The **cytoplasm** comprises the contents of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like **cytosol**, the cytoskeleton, and various chemicals ([\[link\]](#)). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

Microfilaments, intermediate filaments, and microtubules compose a cell's cytoskeleton.

The Cytoskeleton

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that helps to maintain the shape of the cell, secures certain organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently. Collectively, this network of protein fibers is known as the **cytoskeleton**. There are three types of fibers within the cytoskeleton: microfilaments, also known as actin filaments, intermediate filaments, and microtubules ([\[link\]](#)).



Microfilaments are the thinnest of the cytoskeletal fibers and function in moving cellular components, for example, during cell division. They also maintain the structure of microvilli, the extensive folding of the plasma membrane found in cells dedicated to absorption. These components are also common in muscle cells and are responsible for muscle cell contraction. Intermediate filaments are

of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles. Keratin, the compound that strengthens hair and nails, forms one type of intermediate filament. Microtubules are the thickest of the cytoskeletal fibers. These are hollow tubes that can dissolve and reform quickly. Microtubules guide organelle movement and are the structures that pull chromosomes to their poles during cell division. They are also the structural components of flagella and cilia. In cilia and flagella, the microtubules are organized as a circle of nine double microtubules on the outside and two microtubules in the center.

The centrosome is a region near the nucleus of animal cells that functions as a microtubule-organizing center. It contains a pair of centrioles, two structures that lie perpendicular to each other. Each centriole is a cylinder of nine triplets of microtubules.

The centrosome replicates itself before a cell divides, and the centrioles play a role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division is not clear, since cells that have the centrioles removed can still divide, and plant cells, which lack centrioles, are capable of cell division.

Flagella and Cilia

Flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell, (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When **cilia** (singular = cilium) are present, however, they are many in number and extend along the entire surface of the plasma membrane. They are short, hair-like structures that are used to move entire cells (such as paramecium) or move substances along the outer surface of the cell (for example, the cilia of cells lining the fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that move particulate matter toward the throat that mucus has trapped).

The outermost boundary of the nucleus is the nuclear envelope. Notice that the nuclear envelope consists of two phospholipid bilayers (membranes)—an outer membrane and an inner membrane—in contrast to the plasma membrane ([\[link\]](#)), which consists of only one phospholipid bilayer. (credit: modification of work by NIGMS, NIH) The Golgi apparatus in this transmission electron micrograph of a white blood cell is visible as a stack of semicircular flattened rings in the lower portion of this image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell) A macrophage has phagocytized a potentially

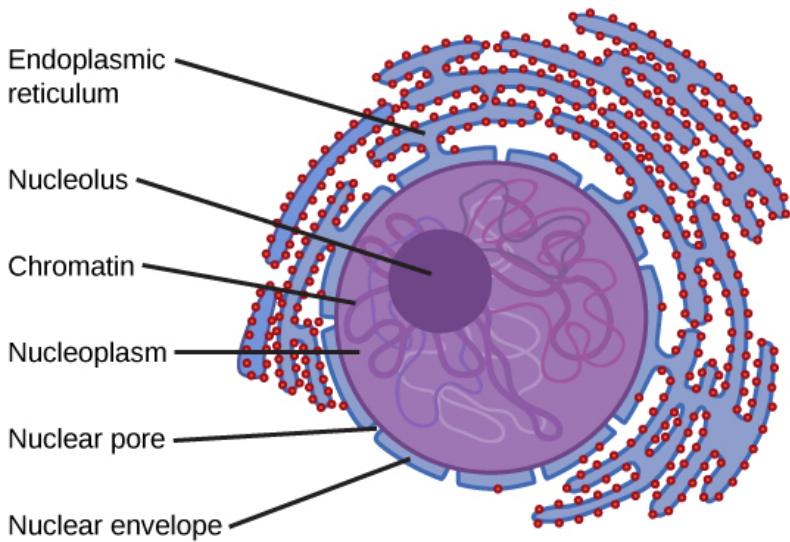
pathogenic bacterium into a vesicle, which then fuses with a lysosome within the cell so that the pathogen can be destroyed. Other organelles are present in the cell, but for simplicity, are not shown.

The Endomembrane System

The **endomembrane system** (*endo* = within) is a group of membranes and organelles ([\[link\]](#)) in eukaryotic cells that work together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell ([\[link\]](#)). The **nucleus** (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins. Let us look at it in more detail ([\[link\]](#)).



The **nuclear envelope** is a double-membrane structure that constitutes the outermost portion of the nucleus ([\[link\]](#)). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and the cytoplasm.

To understand chromatin, it is helpful to first consider chromosomes. Chromosomes are structures within the nucleus that are made up of DNA, the hereditary material, and proteins. This combination of DNA and proteins is called chromatin. In eukaryotes, chromosomes are linear structures. Every species has a specific number of chromosomes in the nucleus of its body cells. For example, in

humans, the chromosome number is 46, whereas in fruit flies, the chromosome number is eight.

Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, the chromosomes resemble an unwound, jumbled bunch of threads.

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus, called the **nucleolus** (plural = nucleoli), aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported through the nuclear pores into the cytoplasm.

The Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** ([\[link\]](#)) is a series of interconnected membranous tubules that collectively modify proteins and synthesize lipids. However, these two functions are performed in separate areas of the endoplasmic reticulum: the rough endoplasmic reticulum and the smooth endoplasmic reticulum, respectively.

The hollow portion of the ER tubules is called the

lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

The **rough endoplasmic reticulum (RER)** is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope.

The ribosomes synthesize proteins while attached to the ER, resulting in transfer of their newly synthesized proteins into the lumen of the RER where they undergo modifications such as folding or addition of sugars. The RER also makes phospholipids for cell membranes.

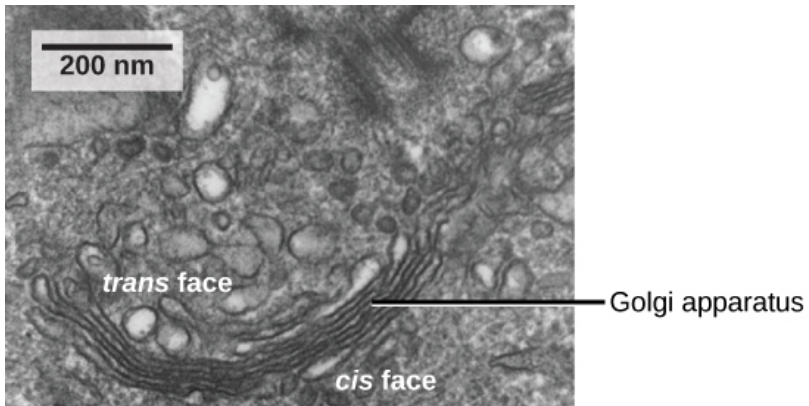
If the phospholipids or modified proteins are not destined to stay in the RER, they will be packaged within vesicles and transported from the RER by budding from the membrane ([\[link\]](#)). Since the RER is engaged in modifying proteins that will be secreted from the cell, it is abundant in cells that secrete proteins, such as the liver.

The **smooth endoplasmic reticulum (SER)** is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see [\[link\]](#)). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and steroid hormones; detoxification of medications and poisons; alcohol metabolism; and storage of calcium

ions.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles need to be sorted, packaged, and tagged so that they wind up in the right place. The sorting, tagging, packaging, and distribution of lipids and proteins take place in the **Golgi apparatus** (also called the Golgi body), a series of flattened membranous sacs ([\[link\]](#)).



The Golgi apparatus has a receiving face near the endoplasmic reticulum and a releasing face on the side away from the ER, toward the cell membrane. The transport vesicles that form from the ER travel to the receiving face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications. The most

frequent modification is the addition of short chains of sugar molecules. The newly modified proteins and lipids are then tagged with small molecular groups to enable them to be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into vesicles that bud from the opposite face of the Golgi. While some of these vesicles, transport vesicles, deposit their contents into other parts of the cell where they will be used, others, secretory vesicles, fuse with the plasma membrane and release their contents outside the cell.

The amount of Golgi in different cell types again illustrates that form follows function within cells. Cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundant number of Golgi.

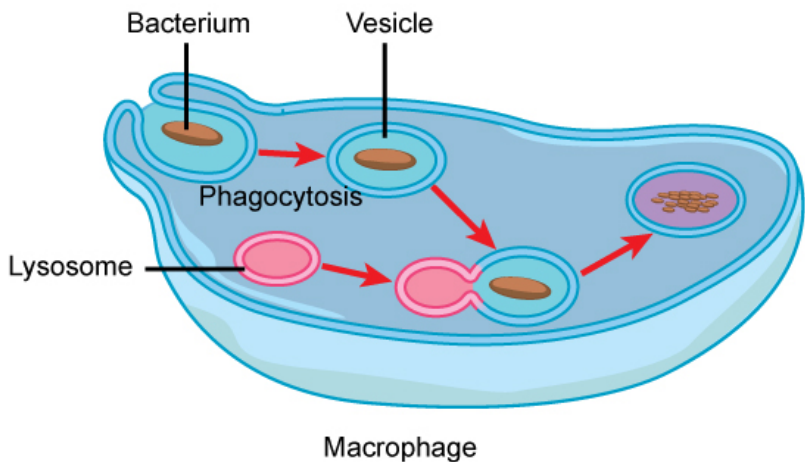
In plant cells, the Golgi has an additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Lysosomes

In animal cells, the **lysosomes** are the cell's "garbage disposal." Digestive enzymes within the

lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. In single-celled eukaryotes, lysosomes are important for digestion of the food they ingest and the recycling of organelles. These enzymes are active at a much lower pH (more acidic) than those located in the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, thus the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Lysosomes also use their hydrolytic enzymes to destroy disease-causing organisms that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen ([\[link\]](#)).

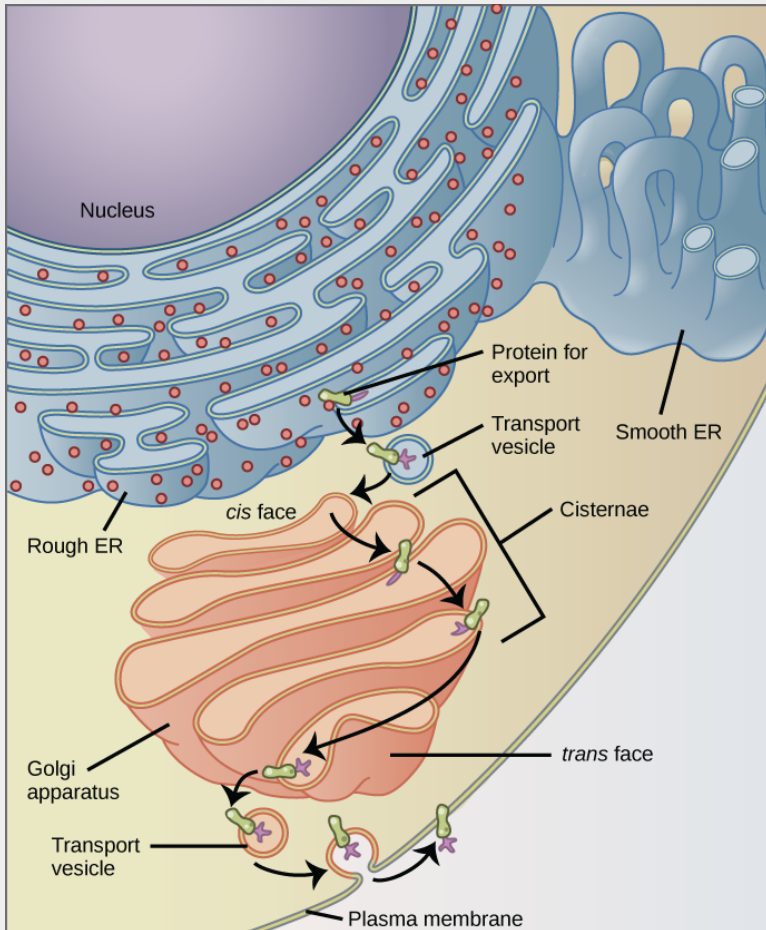


Vesicles and Vacuoles

Vesicles and **vacuoles** are membrane-bound sacs that function in storage and transport. Vacuoles are somewhat larger than vesicles, and the membrane of a vacuole does not fuse with the membranes of other cellular components. Vesicles can fuse with other membranes within the cell system. Additionally, enzymes within plant vacuoles can break down macromolecules.

Art Connection

The endomembrane system works to modify, package, and transport lipids and proteins. (credit: modification of work by Magnus Manske)



Why does the *cis* face of the Golgi not face the plasma membrane?

Ribosomes

Ribosomes are the cellular structures responsible

for protein synthesis. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots floating freely in the cytoplasm. Ribosomes may be attached to either the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum ([link]). Electron microscopy has shown that ribosomes consist of large and small subunits. Ribosomes are enzyme complexes that are responsible for protein synthesis.

Because protein synthesis is essential for all cells, ribosomes are found in practically every cell, although they are smaller in prokaryotic cells. They are particularly abundant in immature red blood cells for the synthesis of hemoglobin, which functions in the transport of oxygen throughout the body.

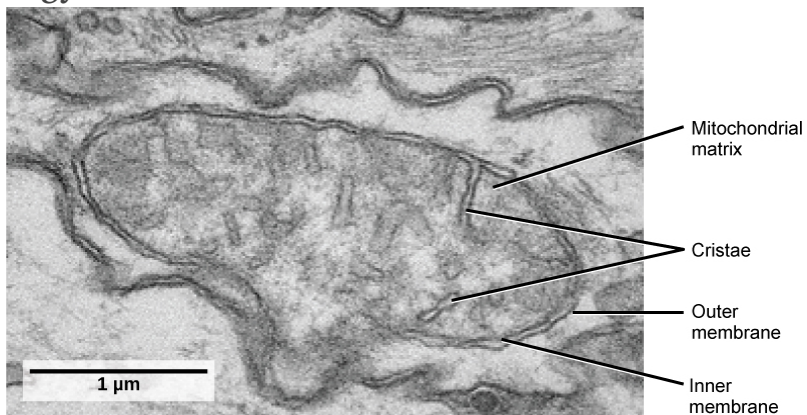
This transmission electron micrograph shows a mitochondrion as viewed with an electron microscope. Notice the inner and outer membranes, the cristae, and the mitochondrial matrix. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main

energy-carrying molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles ([\[link\]](#)) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae, which increase the surface area of the inner membrane. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria because muscle cells need a lot of energy to contract.



Peroxisomes

Peroxisomes are small, round organelles enclosed

by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. Alcohol is detoxified by peroxisomes in liver cells. A byproduct of these oxidation reactions is hydrogen peroxide, H_2O_2 , which is contained within the peroxisomes to prevent the chemical from causing damage to cellular components outside of the organelle. Hydrogen peroxide is safely broken down by peroxisomal enzymes into water and oxygen.

This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma.

Animal Cells versus Plant Cells

Despite their fundamental similarities, there are some striking differences between animal and plant cells (see [\[link\]](#)). Animal cells have centrioles, centrosomes (discussed under the cytoskeleton), and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

The Cell Wall

In [\[link\]b](#), the diagram of a plant cell, you see a structure external to the plasma membrane called

the cell wall. The **cell wall** is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protist cells also have cell walls.

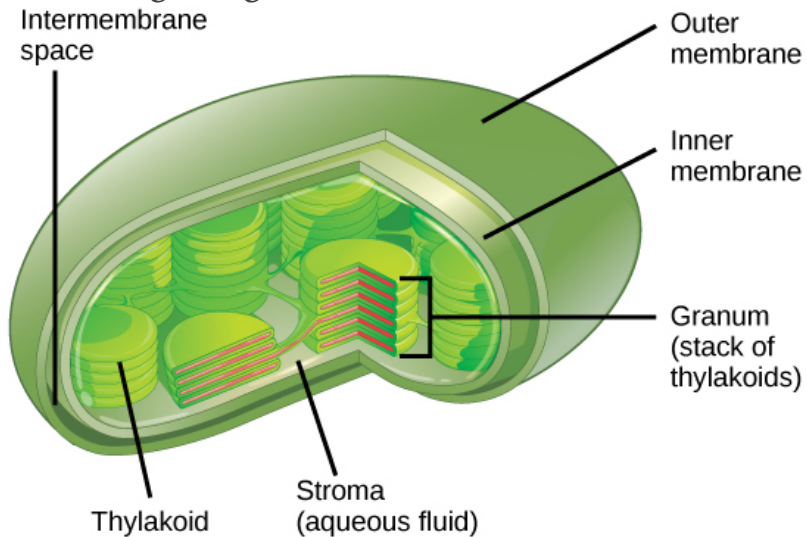
While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose, a polysaccharide made up of long, straight chains of glucose units. When nutritional information refers to dietary fiber, it is referring to the cellulose content of food.

Chloroplasts

Like mitochondria, chloroplasts also have their own DNA and ribosomes. **Chloroplasts** function in photosynthesis and can be found in eukaryotic cells such as plants and algae. In photosynthesis, carbon dioxide, water, and light energy are used to make glucose and oxygen. This is the major difference between plants and animals: Plants (autotrophs) are able to make their own food, like glucose, whereas animals (heterotrophs) must rely on other organisms for their organic compounds or food source.

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids ([\[link\]](#)). Each stack of thylakoids is called a granum (plural = grana). The

fluid enclosed by the inner membrane and surrounding the grana is called the stroma.



The chloroplasts contain a green pigment called chlorophyll, which captures the energy of sunlight for photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria also perform photosynthesis, but they do not have chloroplasts. Their photosynthetic pigments are located in the thylakoid membrane within the cell itself.

Evolution in Action

Endosymbiosis

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why? Strong evidence points to

endosymbiosis as the explanation.

Symbiosis is a relationship in which organisms from two separate species live in close association and typically exhibit specific adaptations to each other. Endosymbiosis (*endo*- = within) is a relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. Microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and are provided a stable habitat and abundant food by living within the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that mitochondria and chloroplasts have DNA and ribosomes, just as bacteria do. Scientists believe that host cells and bacteria formed a mutually beneficial endosymbiotic relationship when the host cells ingested aerobic bacteria and cyanobacteria but did not destroy them. Through evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the photosynthetic bacteria becoming chloroplasts.

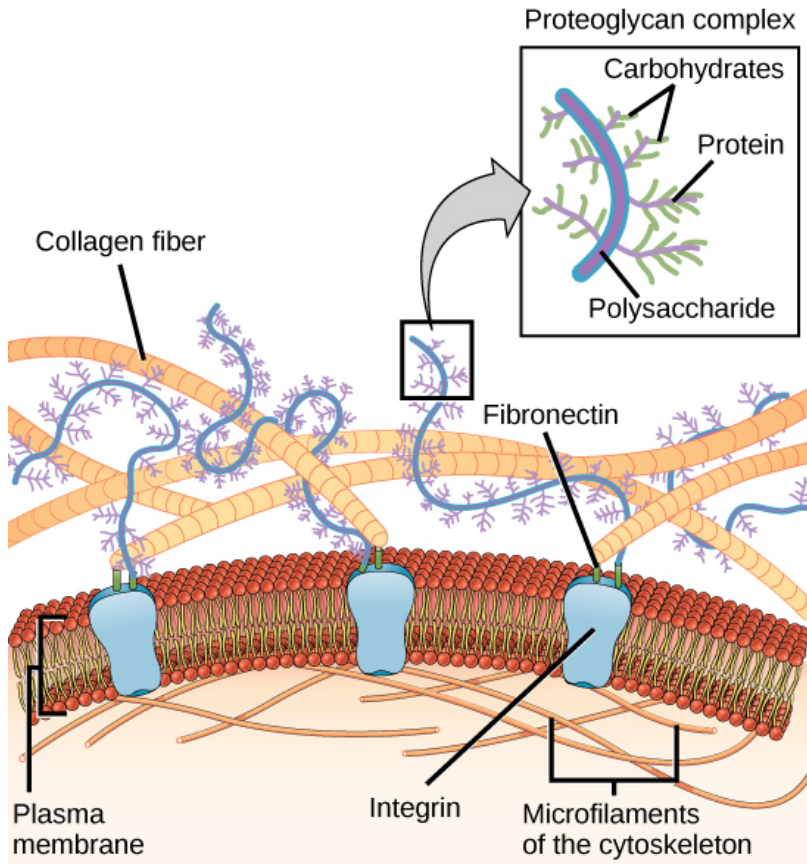
The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at [\[link\]](#), you will see that plant cells each have a large, central vacuole that occupies most of the cell. The **central vacuole** plays a key role in regulating the cell's concentration of water in changing environmental conditions. In plant cells, the liquid inside the central vacuole provides turgor pressure, which is the outward pressure caused by the fluid inside the cell. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That is because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm and into the soil. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of a plant results in the wilted appearance. Additionally, this fluid has a very bitter taste, which discourages consumption by insects and animals. The central vacuole also functions to store proteins in developing seed cells. The extracellular matrix consists of a network of substances secreted by cells.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are glycoproteins and the protein collagen. Collectively, these materials are called the **extracellular matrix** ([\[link\]](#)). Not only does the

extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.



Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates adjacent smooth muscle cells in the blood vessel to

contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

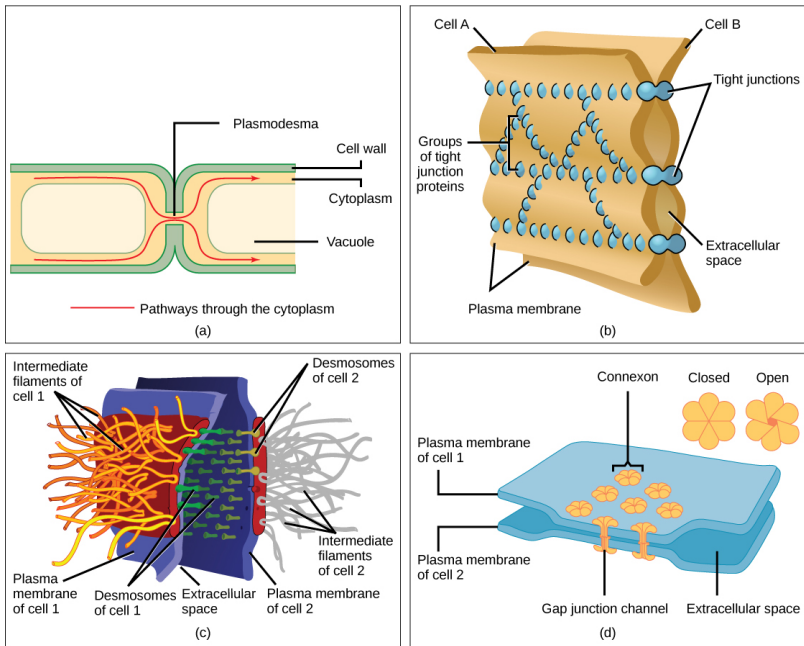
There are four kinds of connections between cells.

(a) A plasmodesma is a channel between the cell walls of two adjacent plant cells. (b) Tight junctions join adjacent animal cells. (c) Desmosomes join two animal cells together. (d) Gap junctions act as channels between animal cells. (credit b, c, d: modification of work by Mariana Ruiz Villareal)

Intercellular Junctions

Cells can also communicate with each other by direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this. **Plasmodesmata** (singular = plasmodesma) are junctions between plant cells, whereas animal cell contacts include tight and gap junctions, and desmosomes.

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell walls surrounding each cell. Plasmodesmata are numerous channels that pass between the cell walls of adjacent plant cells, connecting their cytoplasm and enabling signal molecules and nutrients to be transported from cell to cell ([link](#)a).



A **tight junction** is a watertight seal between two adjacent animal cells ([\[link\]](#)b). Proteins hold the cells tightly against each other. This tight adhesion prevents materials from leaking between the cells. Tight junctions are typically found in the epithelial tissue that lines internal organs and cavities, and composes most of the skin. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space.

Also found only in animal cells are **desmosomes**, which act like spot welds between adjacent epithelial cells ([\[link\]](#)c). They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate ([link](#)d). Structurally, however, gap junctions and plasmodesmata differ.

**Components
of
Prokaryotic
and
Eukaryotic
Cells and
Their
Functions**

Cell Component	Function	Present in Prokaryotes	Present in Animal Cells?	Present in Plant Cells?
----------------	----------	------------------------	--------------------------	-------------------------

Plasma membrane	Separates cell from external environment; controls passage of organic	Yes	Yes	Yes
-----------------	---	-----	-----	-----

molecules,
ions,
water,
oxygen,
and
wastes
into and
out of the
cell

Cytoplasm Provides

Yes

Yes

Yes

structure
to cell;
site of
many
metabolic
reactions;
medium
in which
organelles
are found

Nucleoid

Location
of DNA

Yes

No

No

Nucleus

Cell

No

Yes

Yes

organelle
that
houses
DNA and
directs
synthesis
of
ribosomes

and
proteins
synthesis

Ribosomes	Protein	Yes	Yes	Yes
Mitochondria	ATP	No	Yes	Yes

production/
cellular
respiration

Peroxisomes	Oxidizes	No	Yes	Yes
-------------	----------	----	-----	-----

and
breaks
down
fatty acids
and
amino
acids, and
detoxifies
poisons

Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
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Centrosomes	Unspecified role in cell division in animal cells;	No	Yes	No
-------------	---	----	-----	----

organizing
center of
microtubules
in animal
cells

Lysosomes

Digestion of

No

Yes

No

macromolecules;
recycling
of worn-
out
organelles

Cell wall

Protection, structural support and maintenance of cell shape
Yes, primarily peptidoglycan in bacteria but not Archaea

No

Yes,
primarily
cellulose

Chloroplast

Photosynthesis

No

No

Yes

Endoplasmic reticulum

Modifies proteins

No

Yes

Yes

and synthesizes lipids

Golgi apparatus

Modifies, sorts, tags, packages, and distributes

No

Yes

Yes

lipids and
proteins

Cytoskeleton

Maintains cell's

Yes

Yes

shape,
secures
organelles
in specific
positions,
allows
cytoplasm
and
vesicles to
move
within the
cell, and
enables
unicellular
organisms
to move
independently

Flagella

Cellular
locomotion

Some

Some

No,
except for
some
plant
sperm.

Cilia

Cellular
locomotion,
movement
of
particles

No

Some

No

along
extracellular
surface of
plasma
membrane,
and
filtration

This table provides the components of prokaryotic and eukaryotic cells and their respective functions.

Section Summary

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. The plasma membrane is a phospholipid bilayer embedded with proteins. The nucleolus within the nucleus is the site for ribosome assembly. Ribosomes are found in the cytoplasm or are attached to the cytoplasmic side of the plasma membrane or endoplasmic reticulum. They perform protein synthesis. Mitochondria perform cellular respiration and produce ATP. Peroxisomes break down fatty acids, amino acids, and some toxins. Vesicles and vacuoles are storage and transport compartments. In plant cells, vacuoles

also help break down macromolecules.

Animal cells also have a centrosome and lysosomes. The centrosome has two bodies, the centrioles, with an unknown role in cell division. Lysosomes are the digestive organelles of animal cells.

Plant cells have a cell wall, chloroplasts, and a central vacuole. The plant cell wall, whose primary component is cellulose, protects the cell, provides structural support, and gives shape to the cell. Photosynthesis takes place in chloroplasts. The central vacuole expands, enlarging the cell without the need to produce more cytoplasm.

The endomembrane system includes the nuclear envelope, the endoplasmic reticulum, Golgi apparatus, lysosomes, vesicles, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport membrane lipids and proteins.

The cytoskeleton has three different types of protein elements. Microfilaments provide rigidity and shape to the cell, and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural elements

of centrioles, flagella, and cilia.

Animal cells communicate through their extracellular matrices and are connected to each other by tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other by plasmodesmata.

Art Connections

[\[link\]](#) What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

[\[link\]](#) Plant cells have plasmodesmata, a cell wall, a large central vacuole, chloroplasts, and plastids. Animal cells have lysosomes and centrosomes.

[\[link\]](#) Why does the *cis* face of the Golgi not face the plasma membrane?

[\[link\]](#) Because that face receives chemicals from the ER, which is toward the center of the cell.

Multiple Choice

Which of the following is found both in eukaryotic and prokaryotic cells?

1. nucleus
2. mitochondrion
3. vacuole
4. ribosome

D

Which of the following is not a component of the endomembrane system?

1. mitochondrion
2. Golgi apparatus
3. endoplasmic reticulum
4. lysosome

A

Free Response

In the context of cell biology, what do we mean by form follows function? What are at least two examples of this concept?

“Form follows function” refers to the idea that the function of a body part dictates the form of that body part. As an example, organisms like birds or fish that fly or swim quickly through the air or water have streamlined bodies that reduce drag. At the level of the cell, in tissues involved in secretory functions, such as the salivary glands, the cells have abundant Golgi.

Glossary

cell wall

a rigid cell covering made of cellulose in plants, peptidoglycan in bacteria, non-peptidoglycan compounds in Archaea, and chitin in fungi that protects the cell, provides structural support, and gives shape to the cell

central vacuole

a large plant cell organelle that acts as a storage compartment, water reservoir, and site of macromolecule degradation

chloroplast

a plant cell organelle that carries out photosynthesis

cilium

(plural: cilia) a short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoplasm

the entire region between the plasma membrane and the nuclear envelope, consisting of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals

cytoskeleton

the network of protein fibers that collectively maintains the shape of the cell, secures some organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move

cytosol

the gel-like material of the cytoplasm in which cell structures are suspended

desmosome

a linkage between adjacent epithelial cells that forms when cadherins in the plasma

membrane attach to intermediate filaments

endomembrane system

the group of organelles and membranes in eukaryotic cells that work together to modify, package, and transport lipids and proteins

endoplasmic reticulum (ER)

a series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

extracellular matrix

the material, primarily collagen, glycoproteins, and proteoglycans, secreted from animal cells that holds cells together as a tissue, allows cells to communicate with each other, and provides mechanical protection and anchoring for cells in the tissue

flagellum

(plural: flagella) the long, hair-like structure that extends from the plasma membrane and is used to move the cell

gap junction

a channel between two adjacent animal cells that allows ions, nutrients, and other low-molecular weight substances to pass between the cells, enabling the cells to communicate

Golgi apparatus

a eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

lysosome

an organelle in an animal cell that functions as the cell's digestive component; it breaks down proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles

mitochondria

(singular: mitochondrion) the cellular organelles responsible for carrying out cellular respiration, resulting in the production of ATP, the cell's main energy-carrying molecule

nuclear envelope

the double-membrane structure that constitutes the outermost portion of the nucleus

nucleolus

the darkly staining body within the nucleus that is responsible for assembling ribosomal subunits

nucleus

the cell organelle that houses the cell's DNA and directs the synthesis of ribosomes and proteins

peroxisome

a small, round organelle that contains hydrogen peroxide, oxidizes fatty acids and amino acids, and detoxifies many poisons

plasma membrane

a phospholipid bilayer with embedded (integral) or attached (peripheral) proteins that separates the internal contents of the cell from its surrounding environment

plasmodesma

(plural: plasmodesmata) a channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

ribosome

a cellular structure that carries out protein synthesis

rough endoplasmic reticulum (RER)

the region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification

smooth endoplasmic reticulum (SER)

the region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies chemicals like pesticides, preservatives, medications,

and environmental pollutants, and stores calcium ions

tight junction

a firm seal between two adjacent animal cells created by protein adherence

vacuole

a membrane-bound sac, somewhat larger than a vesicle, that functions in cellular storage and transport

vesicle

a small, membrane-bound sac that functions in cellular storage and transport; its membrane is capable of fusing with the plasma membrane and the membranes of the endoplasmic reticulum and Golgi apparatus

Connections between Cells and Cellular Activities

By the end of this section, you will be able to:

- Describe the extracellular matrix
- List examples of the ways that plant cells and animal cells communicate with adjacent cells
- Summarize the roles of tight junctions, desmosomes, gap junctions, and plasmodesmata

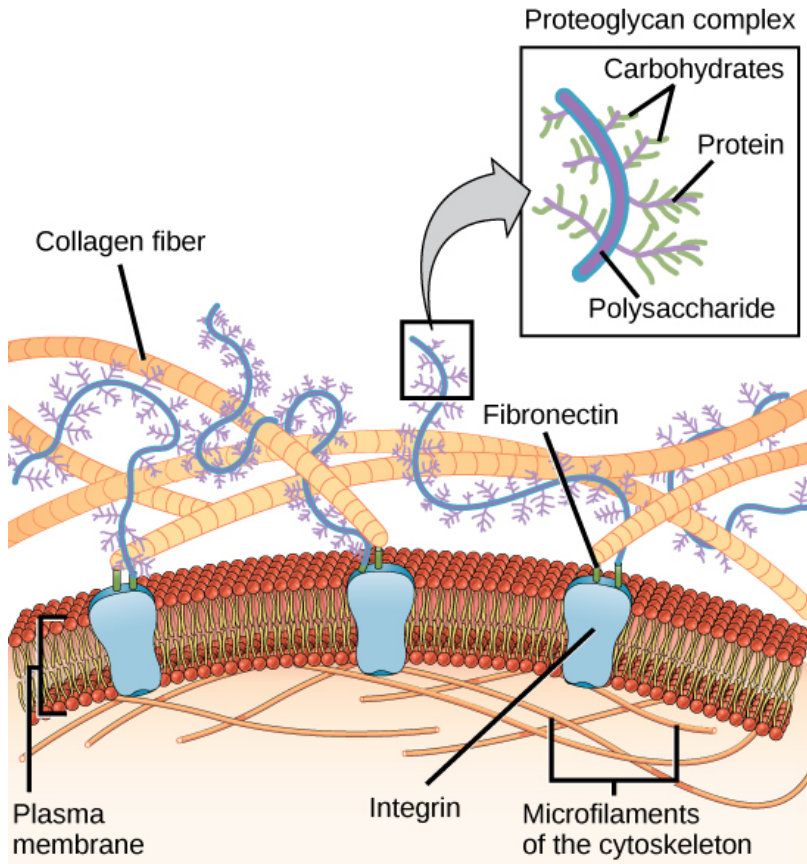
You already know that a group of similar cells working together is called a tissue. As you might expect, if cells are to work together, they must communicate with each other, just as you need to communicate with others if you work on a group project. Let's take a look at how cells communicate with each other.

The extracellular matrix consists of a network of proteins and carbohydrates.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are proteins, and the most abundant protein is collagen. Collagen fibers are interwoven with carbohydrate-containing protein molecules called proteoglycans. Collectively, these materials are called the **extracellular matrix** ([\[link\]](#)). Not only does the extracellular matrix hold the cells

together to form a tissue, but it also allows the cells within the tissue to communicate with each other. How can this happen?



Cells have protein receptors on the extracellular surfaces of their plasma membranes. When a molecule within the matrix binds to the receptor, it changes the molecular structure of the receptor. The receptor, in turn, changes the conformation of the microfilaments positioned just inside the plasma membrane. These conformational changes induce chemical signals inside the cell that reach the

nucleus and turn “on” or “off” the transcription of specific sections of DNA, which affects the production of associated proteins, thus changing the activities within the cell.

Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates the adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

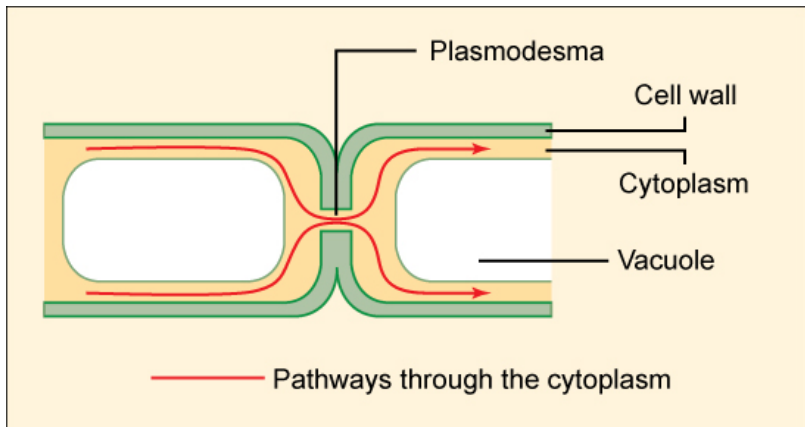
A plasmodesma is a channel between the cell walls of two adjacent plant cells. Plasmodesmata allow materials to pass from the cytoplasm of one plant cell to the cytoplasm of an adjacent cell. Tight junctions form watertight connections between adjacent animal cells. Proteins create tight junction adherence. (credit: modification of work by Mariana Ruiz Villareal) A desmosome forms a very strong spot weld between cells. It is created by the linkage of cadherins and intermediate filaments. (credit: modification of work by Mariana Ruiz Villareal) A gap junction is a protein-lined pore that allows water and small molecules to pass between adjacent animal cells. (credit: modification of work by Mariana Ruiz Villareal)

Intercellular Junctions

Cells can also communicate with each other via direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this. Plasmodesmata are junctions between plant cells, whereas animal cell contacts include tight junctions, gap junctions, and desmosomes.

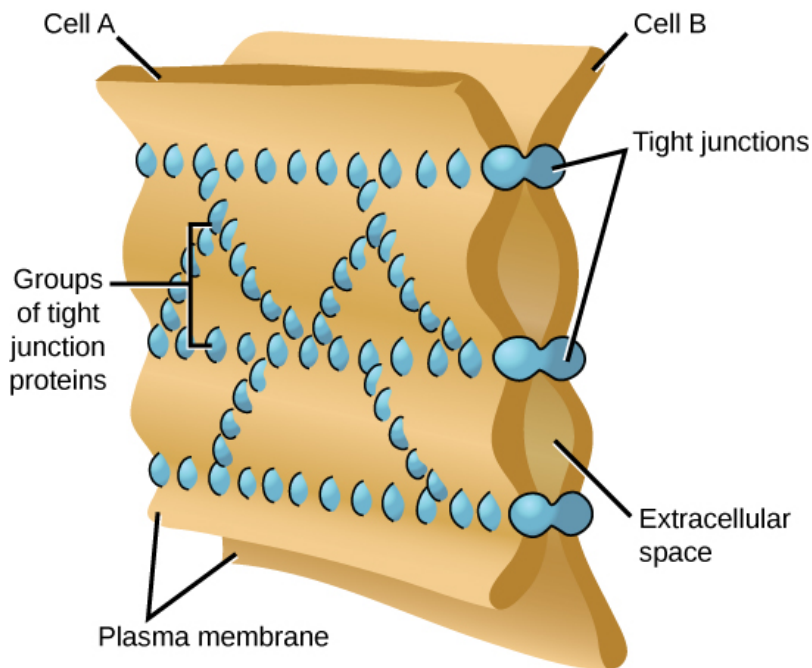
Plasmodesmata

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell wall that surrounds each cell ([link](#)b). How then, can a plant transfer water and other soil nutrients from its roots, through its stems, and to its leaves? Such transport uses the vascular tissues (xylem and phloem) primarily. There also exist structural modifications called **plasmodesmata** (singular = plasmodesma), numerous channels that pass between cell walls of adjacent plant cells, connect their cytoplasm, and enable materials to be transported from cell to cell, and thus throughout the plant ([link](#)).



Tight Junctions

A **tight junction** is a watertight seal between two adjacent animal cells ([link](#)). The cells are held tightly against each other by proteins (predominantly two proteins called claudins and occludins).

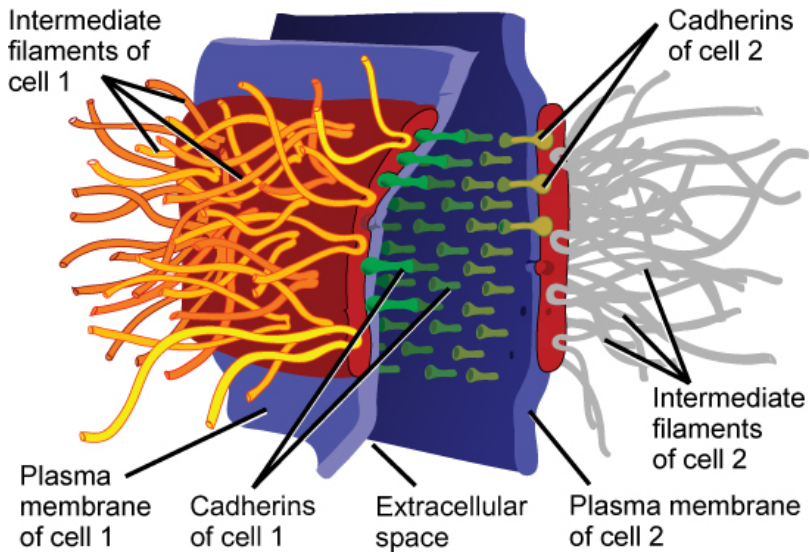


This tight adherence prevents materials from leaking between the cells; tight junctions are typically found in epithelial tissues that line internal organs and cavities, and comprise most of the skin. For example, the tight junctions of the epithelial cells lining your urinary bladder prevent urine from leaking out into the extracellular space.

Desmosomes

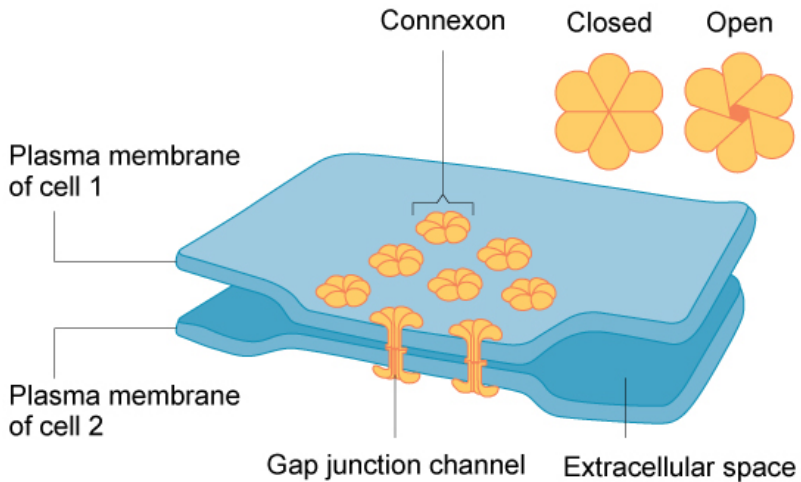
Also found only in animal cells are **desmosomes**, which act like spot welds between adjacent epithelial cells ([\[link\]](#)). Short proteins called cadherins in the plasma membrane connect to intermediate filaments to create desmosomes. The

cadherins join two adjacent cells together and maintain the cells in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.



Gap Junctions

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate ([\[link\]](#)). Structurally, however, gap junctions and plasmodesmata differ.



Gap junctions develop when a set of six proteins (called connexins) in the plasma membrane arrange themselves in an elongated donut-like configuration called a connexon. When the pores (“doughnut holes”) of connexons in adjacent animal cells align, a channel between the two cells forms. Gap junctions are particularly important in cardiac muscle: The electrical signal for the muscle to contract is passed efficiently through gap junctions, allowing the heart muscle cells to contract in tandem.

Link to Learning



To conduct a virtual microscopy lab and review the parts of a cell, work through the steps of this [interactive assignment](#).

Section Summary

Animal cells communicate via their extracellular matrices and are connected to each other via tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other via plasmodesmata.

When protein receptors on the surface of the plasma membrane of an animal cell bind to a substance in the extracellular matrix, a chain of reactions begins that changes activities taking place within the cell. Plasmodesmata are channels between adjacent plant cells, while gap junctions are channels between adjacent animal cells. However, their structures are quite different. A tight junction is a watertight seal

between two adjacent cells, while a desmosome acts like a spot weld.

Review Questions

Which of the following are found only in plant cells?

1. gap junctions
2. desmosomes
3. plasmodesmata
4. tight junctions

C

The key components of desmosomes are cadherins and _____.

1. actin
2. microfilaments
3. intermediate filaments
4. microtubules

C

Free Response

How does the structure of a plasmodesma differ from that of a gap junction?

They differ because plant cell walls are rigid. Plasmodesmata, which a plant cell needs for transportation and communication, are able to allow movement of really large molecules. Gap junctions are necessary in animal cells for transportation and communication.

Explain how the extracellular matrix functions.

The extracellular matrix functions in support and attachment for animal tissues. It also functions in the healing and growth of the tissue.

Glossary

desmosome

linkages between adjacent epithelial cells that form when cadherins in the plasma membrane attach to intermediate filaments

extracellular matrix

material (primarily collagen, glycoproteins, and proteoglycans) secreted from animal cells that provides mechanical protection and anchoring for the cells in the tissue

gap junction

channel between two adjacent animal cells that allows ions, nutrients, and low molecular weight substances to pass between cells, enabling the cells to communicate

plasmodesma

(plural = plasmodesmata) channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

tight junction

firm seal between two adjacent animal cells created by protein adherence

Cell Division

By the end of this section, you will be able to:

- Describe the structure of prokaryotic and eukaryotic genomes
- Distinguish between chromosomes, genes, and traits
- Describe the mechanisms of chromosome compaction

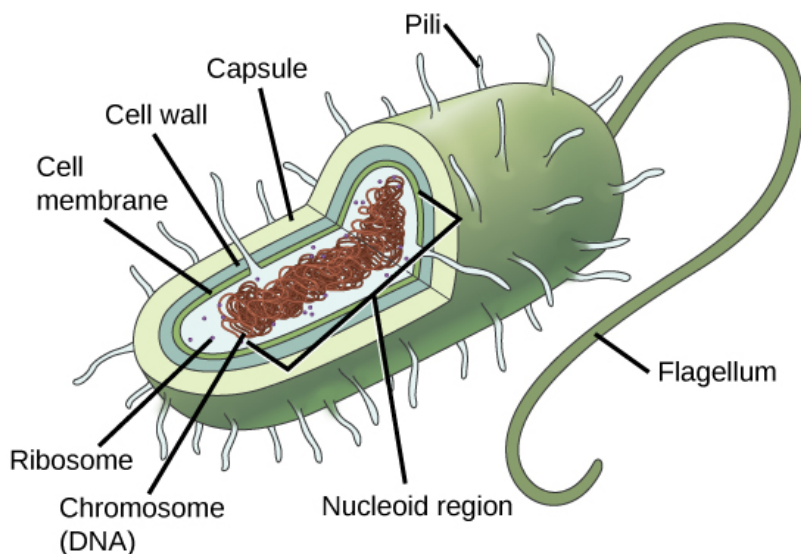
The continuity of life from one cell to another has its foundation in the reproduction of cells by way of the cell cycle. The **cell cycle** is an orderly sequence of events that describes the stages of a cell's life from the division of a single parent cell to the production of two new daughter cells. The mechanisms involved in the cell cycle are highly regulated.

Prokaryotes, including bacteria and archaea, have a single, circular chromosome located in a central region called the nucleoid. There are 23 pairs of homologous chromosomes in a female human somatic cell. The condensed chromosomes are viewed within the nucleus (top), removed from a cell in mitosis and spread out on a slide (right), and artificially arranged according to length (left); an arrangement like this is called a karyotype. In this image, the chromosomes were exposed to fluorescent stains for differentiation of the different chromosomes. A method of staining called “chromosome painting” employs fluorescent dyes

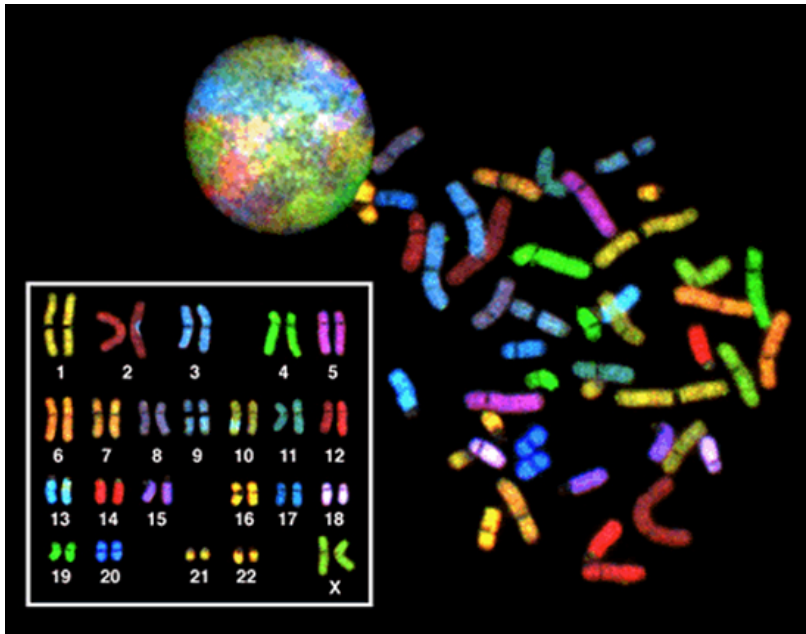
that highlight chromosomes in different colors.
(credit: National Human Genome Project/NIH)

Genomic DNA

Before discussing the steps a cell must undertake to replicate, a deeper understanding of the structure and function of a cell's genetic information is necessary. A cell's DNA, packaged as a double-stranded DNA molecule, is called its **genome**. In prokaryotes, the genome is composed of a single, double-stranded DNA molecule in the form of a loop or circle ([\[link\]](#)). The region in the cell containing this genetic material is called a nucleoid. Some prokaryotes also have smaller loops of DNA called plasmids that are not essential for normal growth. Bacteria can exchange these plasmids with other bacteria, sometimes receiving beneficial new genes that the recipient can add to their chromosomal DNA. Antibiotic resistance is one trait that often spreads through a bacterial colony through plasmid exchange.



In eukaryotes, the genome consists of several double-stranded linear DNA molecules ([\[link\]](#)). Each species of eukaryotes has a characteristic number of chromosomes in the nuclei of its cells. Human body cells have 46 chromosomes, while human **gametes** (sperm or eggs) have 23 chromosomes each. A typical body cell, or somatic cell, contains two matched sets of chromosomes, a configuration known as **diploid**. The letter n is used to represent a single set of chromosomes; therefore, a diploid organism is designated $2n$. Human cells that contain one set of chromosomes are called gametes, or sex cells; these are eggs and sperm, and are designated $1n$, or **haploid**.



Matched pairs of chromosomes in a diploid organism are called **homologous** (“same knowledge”) **chromosomes**. Homologous chromosomes are the same length and have specific nucleotide segments called **genes** in exactly the same location, or **locus**. Genes, the functional units of chromosomes, determine specific characteristics by coding for specific proteins. Traits are the variations of those characteristics. For example, hair color is a characteristic with traits that are blonde, brown, or black.

Each copy of a homologous pair of chromosomes originates from a different parent; therefore, the genes themselves are not identical. The variation of individuals within a species is due to the specific

combination of the genes inherited from both parents. Even a slightly altered sequence of nucleotides within a gene can result in an alternative trait. For example, there are three possible gene sequences on the human chromosome that code for blood type: sequence A, sequence B, and sequence O. Because all diploid human cells have two copies of the chromosome that determines blood type, the blood type (the trait) is determined by which two versions of the marker gene are inherited. It is possible to have two copies of the same gene sequence on both homologous chromosomes, with one on each (for example, AA, BB, or OO), or two different sequences, such as AB.

Minor variations of traits, such as blood type, eye color, and handedness, contribute to the natural variation found within a species. However, if the entire DNA sequence from any pair of human homologous chromosomes is compared, the difference is less than one percent. The sex chromosomes, X and Y, are the single exception to the rule of homologous chromosome uniformity: Other than a small amount of homology that is necessary to accurately produce gametes, the genes found on the X and Y chromosomes are different.

Double-stranded DNA wraps around histone proteins to form nucleosomes that have the appearance of “beads on a string.” The nucleosomes are coiled into a 30-nm chromatin fiber. When a cell undergoes mitosis, the chromosomes condense even

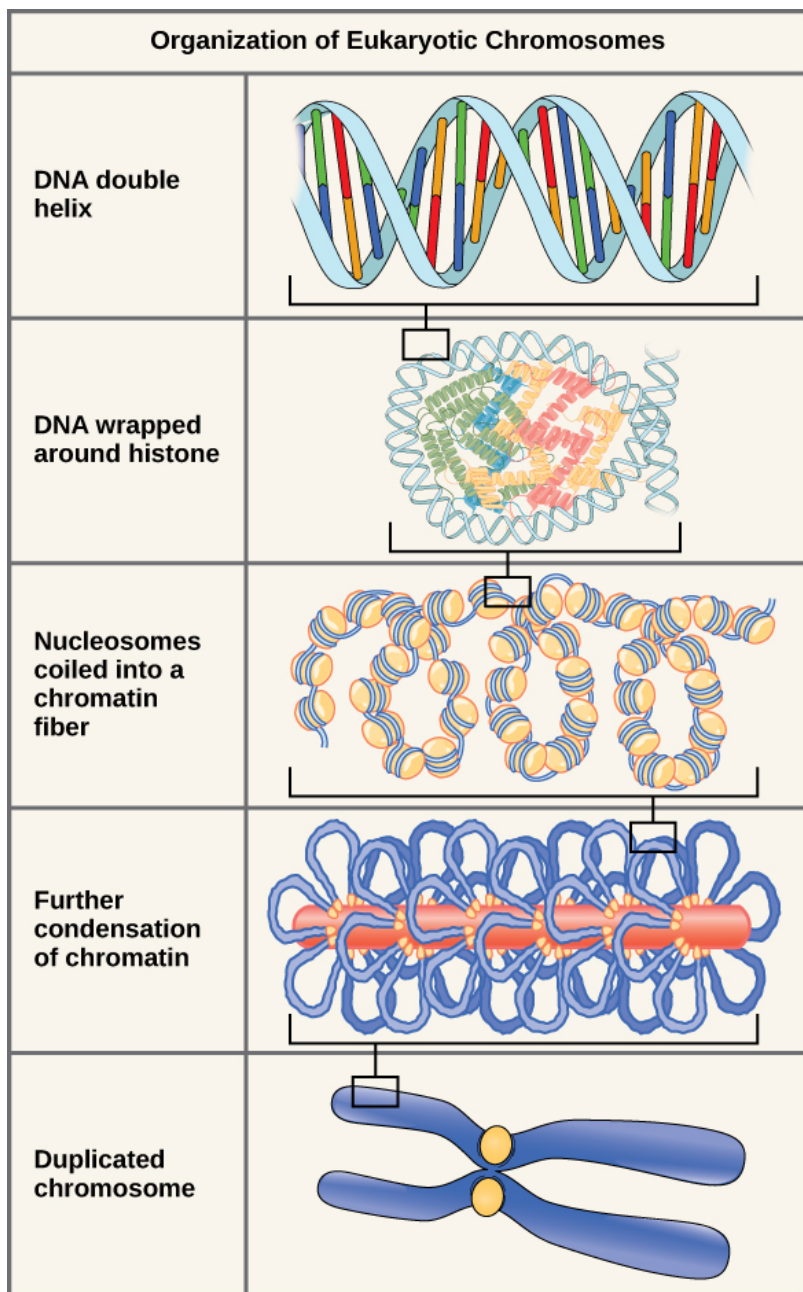
further.

Eukaryotic Chromosomal Structure and Compaction

If the DNA from all 46 chromosomes in a human cell nucleus was laid out end to end, it would measure approximately two meters; however, its diameter would be only 2 nm. Considering that the size of a typical human cell is about 10 μm (100,000 cells lined up to equal one meter), DNA must be tightly packaged to fit in the cell's nucleus. At the same time, it must also be readily accessible for the genes to be expressed. During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes. There are a number of ways that chromosomes are compacted.

In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight **histone proteins** at regular intervals along the entire length of the chromosome ([\[link\]](#)). The DNA-histone complex is called chromatin. The beadlike, histone DNA complex is called a **nucleosome**, and DNA connecting the nucleosomes is called linker DNA. A DNA molecule in this form is about seven times shorter than the double helix without the histones, and the beads are about 10 nm in diameter, in contrast with the 2-nm diameter of a DNA double helix. The next level of compaction occurs as the nucleosomes and the linker DNA

between them are coiled into a 30-nm chromatin fiber. This coiling further shortens the chromosome so that it is now about 50 times shorter than the extended form. In the third level of packing, a variety of fibrous proteins is used to pack the chromatin. These fibrous proteins also ensure that each chromosome in a non-dividing cell occupies a particular area of the nucleus that does not overlap with that of any other chromosome (see the top image in [\[link\]](#)).



DNA replicates in the S phase of interphase. After replication, the chromosomes are composed of two

linked sister **chromatids**. When fully compact, the pairs of identically packed chromosomes are bound to each other by cohesin proteins. The connection between the sister chromatids is closest in a region called the **centromere**. The conjoined sister chromatids, with a diameter of about 1 μm , are visible under a light microscope. The centromeric region is highly condensed and thus will appear as a constricted area.

Link to Learning



This animation illustrates the different levels of chromosome packing.

https://www.openstaxcollege.org/1/Packaged_DNA

Section Summary

Prokaryotes have a single circular chromosome composed of double-stranded DNA, whereas eukaryotes have multiple, linear chromosomes composed of chromatin surrounded by a nuclear membrane. The 46 chromosomes of human somatic cells are composed of 22 pairs of autosomes (matched pairs) and a pair of sex chromosomes, which may or may not be matched. This is the $2n$ or diploid state. Human gametes have 23 chromosomes or one complete set of chromosomes; a set of chromosomes is complete with either one of the sex chromosomes. This is the n or haploid state. Genes are segments of DNA that code for a specific protein. An organism's traits are determined by the genes inherited from each parent. Duplicated chromosomes are composed of two sister chromatids. Chromosomes are compacted using a variety of mechanisms during certain stages of the cell cycle. Several classes of protein are involved in the organization and packing of the chromosomal DNA into a highly condensed structure. The condensing complex compacts chromosomes, and the resulting condensed structure is necessary for chromosomal segregation during mitosis.

Review Questions

A diploid cell has_____ the number of chromosomes as a haploid cell.

1. one-fourth
2. half
3. twice
4. four times

C

An organism's traits are determined by the specific combination of inherited ____.

1. cells.
2. genes.
3. proteins.
4. chromatids.

B

The first level of DNA organization in a eukaryotic cell is maintained by which molecule?

1. cohesin
2. condensin
3. chromatin
4. histone

D

Identical copies of chromatin held together by cohesin at the centromere are called ____.

1. histones.
2. nucleosomes.
3. chromatin.
4. sister chromatids.

D

Free Response

Compare and contrast a human somatic cell to a human gamete.

Human somatic cells have 46 chromosomes: 22 pairs and 2 sex chromosomes that may or may not form a pair. This is the $2n$ or diploid condition. Human gametes have 23 chromosomes, one each of 23 unique chromosomes, one of which is a sex chromosome. This is the n or haploid condition.

What is the relationship between a genome, chromosomes, and genes?

The genome consists of the sum total of an organism's chromosomes. Each chromosome contains hundreds and sometimes thousands of genes, segments of DNA that code for a polypeptide or RNA, and a large amount of DNA with no known function.

Eukaryotic chromosomes are thousands of times longer than a typical cell. Explain how chromosomes can fit inside a eukaryotic nucleus.

The DNA double helix is wrapped around histone proteins to form structures called nucleosomes. Nucleosomes and the linker DNA in between them are coiled into a 30-nm fiber. During cell division, chromatin is further condensed by packing proteins.

Glossary

cell cycle

ordered sequence of events that a cell passes through between one cell division and the next

centromere

region at which sister chromatids are bound together; a constricted area in condensed chromosomes

chromatid

single DNA molecule of two strands of duplicated DNA and associated proteins held together at the centromere

diploid

cell, nucleus, or organism containing two sets of chromosomes ($2n$)

gamete

haploid reproductive cell or sex cell (sperm, pollen grain, or egg)

gene

physical and functional unit of heredity, a sequence of DNA that codes for a protein.

genome

total genetic information of a cell or organism

haploid

cell, nucleus, or organism containing one set of chromosomes (n)

histone

one of several similar, highly conserved, low molecular weight, basic proteins found in the

chromatin of all eukaryotic cells; associates with DNA to form nucleosomes

homologous chromosomes

chromosomes of the same morphology with genes in the same location; diploid organisms have pairs of homologous chromosomes (homologs), with each homolog derived from a different parent

locus

position of a gene on a chromosome

nucleosome

subunit of chromatin composed of a short length of DNA wrapped around a core of histone proteins

Prokaryotic Cell Division

By the end of this section, you will be able to:

- Describe the process of binary fission in prokaryotes
- Explain how FtsZ and tubulin proteins are examples of homology

Prokaryotes, such as bacteria, propagate by binary fission. For unicellular organisms, cell division is the only method to produce new individuals. In both prokaryotic and eukaryotic cells, the outcome of cell reproduction is a pair of daughter cells that are genetically identical to the parent cell. In unicellular organisms, daughter cells are individuals.

To achieve the outcome of cloned offspring, certain steps are essential. The genomic DNA must be replicated and then allocated into the daughter cells; the cytoplasmic contents must also be divided to give both new cells the machinery to sustain life. In bacterial cells, the genome consists of a single, circular DNA chromosome; therefore, the process of cell division is simplified. Karyokinesis is unnecessary because there is no nucleus and thus no need to direct one copy of the multiple chromosomes into each daughter cell. This type of cell division is called **binary (prokaryotic) fission**.

These images show the steps of binary fission in prokaryotes. (credit: modification of work by “Mcstrother”/Wikimedia Commons)

Binary Fission

Due to the relative simplicity of the prokaryotes, the cell division process, called binary fission, is a less complicated and much more rapid process than cell division in eukaryotes. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell ([\[link\]](#)). Although the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size, there are no histone proteins and thus no nucleosomes in prokaryotes. The packing proteins of bacteria are, however, related to the cohesin and condensin proteins involved in the chromosome compaction of eukaryotes.

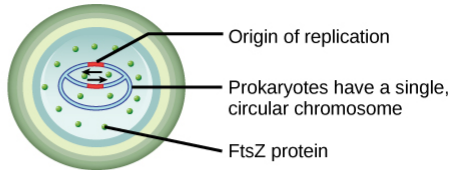
The bacterial chromosome is attached to the plasma membrane at about the midpoint of the cell. The starting point of replication, the **origin**, is close to the binding site of the chromosome to the plasma membrane ([\[link\]](#)). Replication of the DNA is bidirectional, moving away from the origin on both strands of the loop simultaneously. As the new double strands are formed, each origin point moves away from the cell wall attachment toward the opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes. After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. The formation of a ring composed

of repeating units of a protein called **FtsZ** directs the partition between the nucleoids. Formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell wall materials to the site. A **septum** is formed between the nucleoids, extending gradually from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

Binary Fission in Prokaryotes

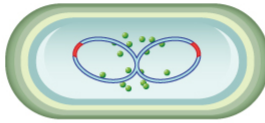
Replication of the circular prokaryotic chromosome begins at the origin of replication and continues in both directions at once.

1



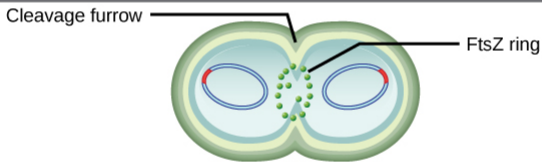
The cell begins to elongate. FtsZ proteins migrate toward the midpoint of the cell.

2



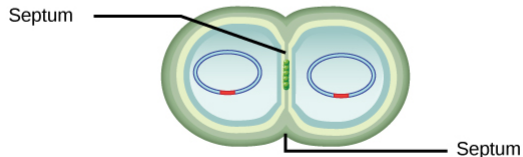
The duplicated chromosomes separate and continue to move away from each other toward opposite ends of the cell. FtsZ proteins form a ring around the periphery of the midpoint between the chromosomes.

3



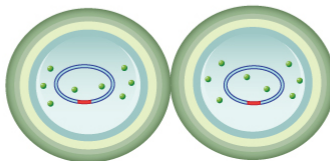
The FtsZ ring directs the formation of a septum that divides the cell. Plasma membrane and cell wall materials accumulate.

4



After the septum is complete, the cell pinches in two, forming two daughter cells. FtsZ is dispersed throughout the cytoplasm of the new cells.

5



Evolution Connection

Mitotic Spindle Apparatus

The precise timing and formation of the mitotic spindle is critical to the success of eukaryotic cell division. Prokaryotic cells, on the other hand, do not undergo karyokinesis and therefore have no need for a mitotic spindle. However, the FtsZ protein that plays such a vital role in prokaryotic cytokinesis is structurally and functionally very similar to tubulin, the building block of the microtubules that make up the mitotic spindle fibers that are necessary for eukaryotes. FtsZ proteins can form filaments, rings, and other three-dimensional structures that resemble the way tubulin forms microtubules, centrioles, and various cytoskeletal components. In addition, both FtsZ and tubulin employ the same energy source, GTP (guanosine triphosphate), to rapidly assemble and disassemble complex structures.

FtsZ and tubulin are homologous structures derived from common evolutionary origins. In this example, FtsZ is the ancestor protein to tubulin (a modern protein). While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since evolving from its FtsZ prokaryotic origin. A survey of mitotic assembly components found in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex membrane-enclosed genomes of multicellular eukaryotes ([\[link\]](#)).

Cell Division Apparatus among Various Organisms

	Structure of genetic material	Division of nuclear material	Separation of daughter cells
Prokaryotes	There is no nucleus. The single, circular chromosome exists in a region of cytoplasm called the nucleoid.	Occurs through binary fission. As the chromosome is replicated, the two copies move to opposite ends of the cell by an unknown mechanism.	FtsZ proteins assemble into a ring that pinches the cell in two.
Some protists	Linear chromosomes exist in the nucleus.	Chromosomes attach to the nuclear envelope, which remains intact. The mitotic	Microfilaments form a cleavage furrow that pinches the cell in two.

spindle
passes
through the
envelope
and
elongates
the cell. No
centrioles
exist.

Other
protists

Linear
chromosomes
exist in the
nucleus.

A mitotic
spindle
forms from
the
centrioles
and passes
through the
nuclear
membrane,
which
remains
intact.
Chromosomes
attach to the
mitotic
spindle,
which
separates
the
chromosomes
and
elongates

Microfilaments
form a
cleavage
furrow that
pinches the
cell in two.

Animal cells	Linear chromosomes exist in the nucleus.	the cell. A mitotic spindle forms from the centrosomes. The nuclear envelope dissolves. Chromosomes attach to the mitotic spindle, which separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.
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Section Summary

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and then each copy is allocated into a daughter cell. In addition, the cytoplasmic contents are divided evenly and

distributed to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome but no nucleus.

Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. Ingrowth of membrane and cell wall material from the periphery of the cells results in the formation of a septum that eventually constructs the separate cell walls of the daughter cells.

Review Questions

Which eukaryotic cell cycle event is missing in binary fission?

1. cell growth
2. DNA duplication
3. karyokinesis
4. cytokinesis

C

FtsZ proteins direct the formation of a _____ that will eventually form the new cell walls of the daughter cells.

1. contractile ring
 2. cell plate
 3. cytoskeleton
 4. septum
-

B

Free Response

Name the common components of eukaryotic cell division and binary fission.

The common components of eukaryotic cell division and binary fission are DNA duplication, segregation of duplicated chromosomes, and division of the cytoplasmic contents.

Describe how the duplicated bacterial chromosomes are distributed into new daughter cells without the direction of the mitotic spindle.

As the chromosome is being duplicated, each origin moves away from the starting point of replication. The chromosomes are attached to

the cell membrane via proteins; the growth of the membrane as the cell elongates aids in their movement.

Glossary

binary fission

prokaryotic cell division process

FtsZ

tubulin-like protein component of the prokaryotic cytoskeleton that is important in prokaryotic cytokinesis (name origin: Filamenting temperature-sensitive mutant Z)

origin

(also, ORI) region of the prokaryotic chromosome where replication begins (origin of replication)

septum

structure formed in a bacterial cell as a precursor to the separation of the cell into two daughter cells

The Cell Cycle

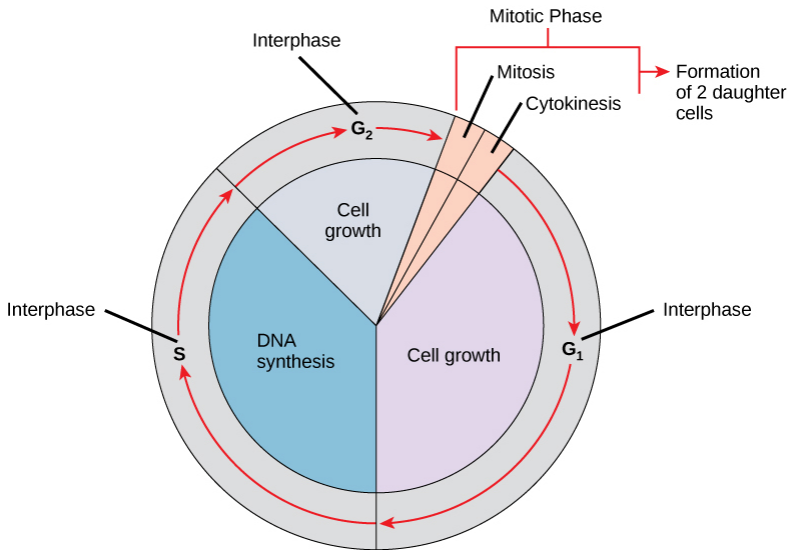
By the end of this section, you will be able to:

- Describe the three stages of interphase
- Discuss the behavior of chromosomes during mitosis and how the cytoplasmic content divides during cytokinesis
- Define the quiescent G₀ phase
- Explain how the three internal control checkpoints occur at the end of G₁, at the G₂–M transition, and during metaphase

The **cell cycle** is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produce two genetically identical cells. The cell cycle has two major phases: interphase and the mitotic phase ([link]). During **interphase**, the cell grows and DNA is replicated. During the **mitotic phase**, the replicated DNA and cytoplasmic contents are separated and the cell divides. Watch this video about the cell cycle: <https://www.youtube.com/watch?v=Wy3N5NCZBHQ>

A cell moves through a series of phases in an orderly manner. During interphase, G₁ involves cell growth and protein synthesis, the S phase involves DNA replication and the replication of the centrosome, and G₂ involves further growth and protein

synthesis. The mitotic phase follows interphase. Mitosis is nuclear division during which duplicated chromosomes are segregated and distributed into daughter nuclei. Usually the cell will divide after mitosis in a process called cytokinesis in which the cytoplasm is divided and two daughter cells are formed.



Interphase

During interphase, the cell undergoes normal processes while also preparing for cell division. For a cell to move from interphase to the mitotic phase, many internal and external conditions must be met. The three stages of interphase are called G₁, S, and G₂.

G₁ Phase

The first stage of interphase is called the **G₁ phase**, or first gap, because little change is visible.

However, during the G₁ stage, the cell is quite active at the biochemical level. The cell is accumulating the building blocks of chromosomal DNA and the associated proteins, as well as accumulating enough energy reserves to complete the task of replicating each chromosome in the nucleus.

S Phase

Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. In the **S phase** (synthesis phase), DNA replication results in the formation of two identical copies of each chromosome—sister chromatids—that are firmly attached at the centromere region. At this stage, each chromosome is made of two sister chromatids and is a duplicated chromosome. The centrosome is duplicated during the S phase. The two centrosomes will give rise to the **mitotic spindle**, the apparatus that orchestrates the movement of chromosomes during mitosis. The centrosome consists of a pair of rod-like **centrioles** at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of many eukaryotic species, such as plants and most fungi.

G₂ Phase

In the **G₂ phase**, or second gap, the cell replenishes its energy stores and synthesizes the proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic spindle. There may be additional cell growth during G₂. The final preparations for the mitotic phase must be completed before the cell is able to enter the first stage of mitosis.

In part (a), a cleavage furrow forms at the former metaphase plate in the animal cell. The plasma membrane is drawn in by a ring of actin fibers contracting just inside the membrane. The cleavage furrow deepens until the cells are pinched in two. In part (b), Golgi vesicles coalesce at the former metaphase plate in a plant cell. The vesicles fuse and form the cell plate. The cell plate grows from the center toward the cell walls. New cell walls are made from the vesicle contents.

The Mitotic Phase

To make two daughter cells, the contents of the nucleus and the cytoplasm must be divided. The mitotic phase is a multistep process during which the duplicated chromosomes are aligned, separated, and moved to opposite poles of the cell, and then the cell is divided into two new identical daughter cells. The first portion of the mitotic phase, **mitosis**, is composed of five stages, which accomplish nuclear division. The second portion of the mitotic


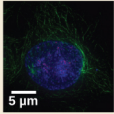

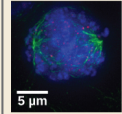

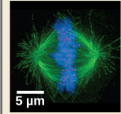
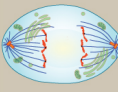
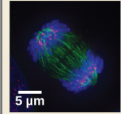
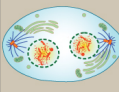
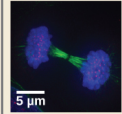
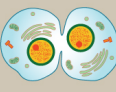
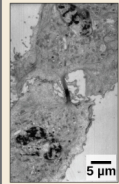
phase, called cytokinesis, is the physical separation of the cytoplasmic components into two daughter cells.

Mitosis

Mitosis is divided into a series of phases—prophase, prometaphase, metaphase, anaphase, and telophase—that result in the division of the cell nucleus ([link](#)).

Art Connection

Animal cell mitosis is divided into five stages—prophase, prometaphase, metaphase, anaphase, and telophase—visualized here by light microscopy with fluorescence. Mitosis is usually accompanied by cytokinesis, shown here by a transmission electron microscope. (credit "diagrams": modification of work by Mariana Ruiz Villareal; credit "mitosis micrographs": modification of work by Roy van Heesbeen; credit "cytokinesis micrograph": modification of work by the Wadsworth Center, NY State Department of Health; donated to the Wikimedia foundation; scale-bar data from Matt Russell)

Prophase	Prometaphase	Metaphase	Anaphase	Telophase	Cytokinesis
 <ul style="list-style-type: none"> Chromosomes condense and become visible Spindle fibers emerge from the centrosomes Nuclear envelope breaks down Centrosomes move toward opposite poles 	 <ul style="list-style-type: none"> Chromosomes continue to condense Kinetochores appear at the centromeres Mitotic spindle microtubules attach to kinetochores 	 <ul style="list-style-type: none"> Chromosomes are lined up at the metaphase plate Each sister chromatid is attached to a spindle fiber originating from opposite poles 	 <ul style="list-style-type: none"> Centromeres split in two Sister chromatids (now called chromosomes) are pulled toward opposite poles Certain spindle fibers begin to elongate the cell 	 <ul style="list-style-type: none"> Chromosomes arrive at opposite poles and begin to decondense Nuclear envelope material surrounds each set of chromosomes The mitotic spindle breaks down Spindle fibers continue to push poles apart 	 <ul style="list-style-type: none"> Animal cells: a cleavage furrow separates the daughter cells Plant cells: a cell plate, the precursor to a new cell wall, separates the daughter cells 

MITOSIS

Which of the following is the correct order of events in mitosis?

1. Sister chromatids line up at the metaphase plate. The kinetochore becomes attached to the mitotic spindle. The nucleus re-forms and the cell divides. The sister chromatids separate.
2. The kinetochore becomes attached to the mitotic spindle. The sister chromatids separate. Sister chromatids line up at the metaphase plate. The nucleus re-forms and the cell divides.
3. The kinetochore becomes attached to metaphase plate. Sister chromatids line up at the metaphase plate. The kinetochore breaks down and the sister chromatids separate. The nucleus re-forms and the cell divides.

4. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks apart and the sister chromatids separate. The nucleus re-forms and the cell divides.

During **prophase**, the “first phase,” several events must occur to provide access to the chromosomes in the nucleus. The nuclear envelope starts to break into small vesicles, and the Golgi apparatus and endoplasmic reticulum fragment and disperse to the periphery of the cell. The nucleolus disappears. The centrosomes begin to move to opposite poles of the cell. The microtubules that form the basis of the mitotic spindle extend between the centrosomes, pushing them farther apart as the microtubule fibers lengthen. The sister chromatids begin to coil more tightly and become visible under a light microscope.

During **prometaphase**, many processes that were begun in prophase continue to advance and culminate in the formation of a connection between the chromosomes and cytoskeleton. The remnants of the nuclear envelope disappear. The mitotic spindle continues to develop as more microtubules assemble and stretch across the length of the former nuclear area. Chromosomes become more condensed and visually discrete. Each sister chromatid attaches to spindle microtubules at the centromere via a protein

complex called the **kinetochore**.

During **metaphase**, all of the chromosomes are aligned in a plane called the **metaphase plate**, or the equatorial plane, midway between the two poles of the cell. The sister chromatids are still tightly attached to each other. At this time, the chromosomes are maximally condensed.

During **anaphase**, the sister chromatids at the equatorial plane are split apart at the centromere. Each chromatid, now called a chromosome, is pulled rapidly toward the centrosome to which its microtubule was attached. The cell becomes visibly elongated as the non-kinetochore microtubules slide against each other at the metaphase plate where they overlap.

During **telophase**, all of the events that set up the duplicated chromosomes for mitosis during the first three phases are reversed. The chromosomes reach the opposite poles and begin to decondense (unravel). The mitotic spindles are broken down into monomers that will be used to assemble cytoskeleton components for each daughter cell. Nuclear envelopes form around chromosomes.

Concept in Action



[This page of movies](#) illustrates different aspects of mitosis. Watch the movie entitled “DIC microscopy of cell division in a newt lung cell” and identify the phases of mitosis.

Cytokinesis

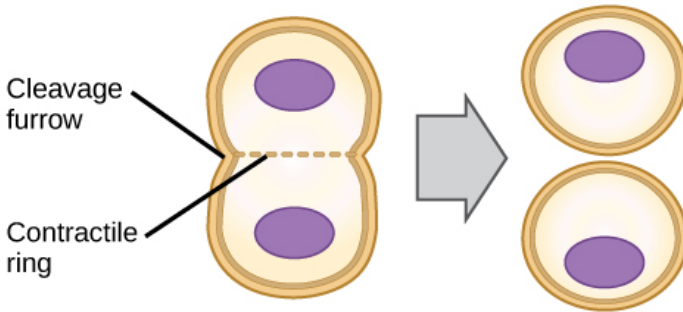
Cytokinesis is the second part of the mitotic phase during which cell division is completed by the physical separation of the cytoplasmic components into two daughter cells. Although the stages of mitosis are similar for most eukaryotes, the process of cytokinesis is quite different for eukaryotes that have cell walls, such as plant cells.

In cells such as animal cells that lack cell walls, cytokinesis begins following the onset of anaphase. A contractile ring composed of actin filaments forms just inside the plasma membrane at the former metaphase plate. The actin filaments pull the equator of the cell inward, forming a fissure. This fissure, or “crack,” is called the **cleavage furrow**. The furrow deepens as the actin ring contracts, and

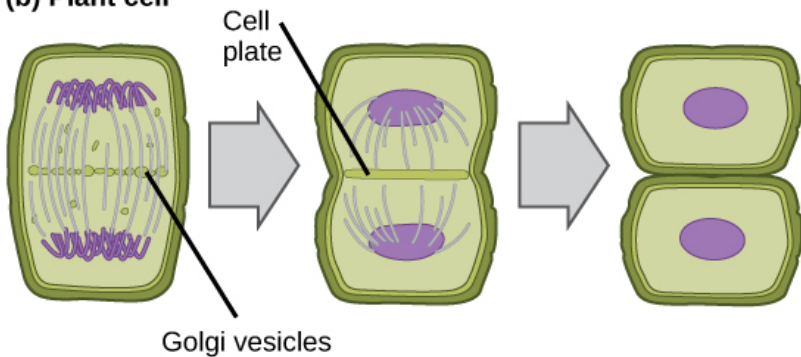
eventually the membrane and cell are cleaved in two ([\[link\]](#)).

In plant cells, a cleavage furrow is not possible because of the rigid cell walls surrounding the plasma membrane. A new cell wall must form between the daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules prior to breaking up into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles move on microtubules to collect at the metaphase plate. There, the vesicles fuse from the center toward the cell walls; this structure is called a **cell plate**. As more vesicles fuse, the cell plate enlarges until it merges with the cell wall at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall of cellulose. The Golgi membranes become the plasma membrane on either side of the new cell wall ([\[link\]](#)).

(a) Animal cell



(b) Plant cell

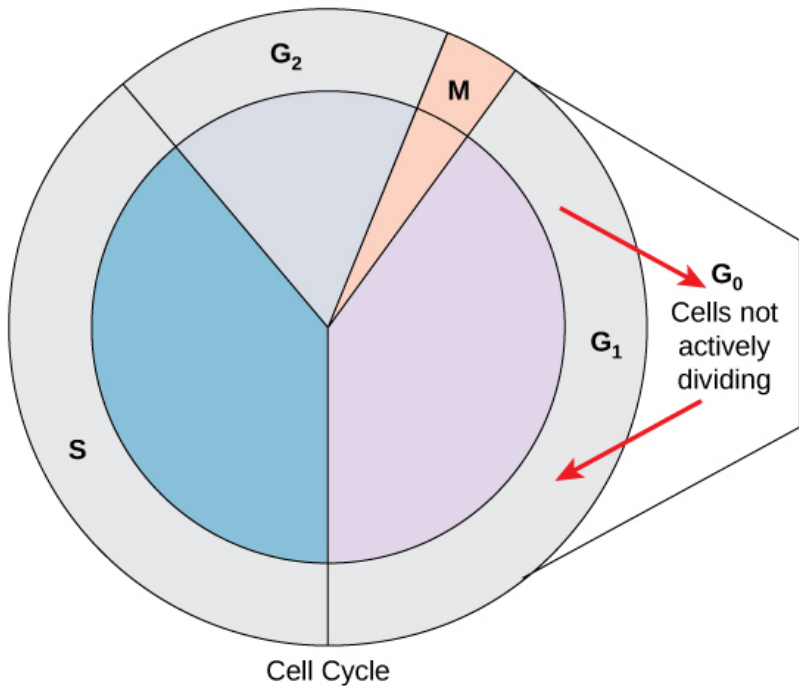


Cells that are not actively preparing to divide enter an alternate phase called G_0 . In some cases, this is a temporary condition until triggered to enter G_1 . In other cases, the cell will remain in G_0 permanently.

G_0 Phase

Not all cells adhere to the classic cell-cycle pattern in which a newly formed daughter cell immediately enters interphase, closely followed by the mitotic phase. Cells in the **G_0 phase** are not actively preparing to divide. The cell is in a quiescent (inactive) stage, having exited the cell cycle. Some

cells enter G_0 temporarily until an external signal triggers the onset of G_1 . Other cells that never or rarely divide, such as mature cardiac muscle and nerve cells, remain in G_0 permanently ([\[link\]](#)).



Control of the Cell Cycle

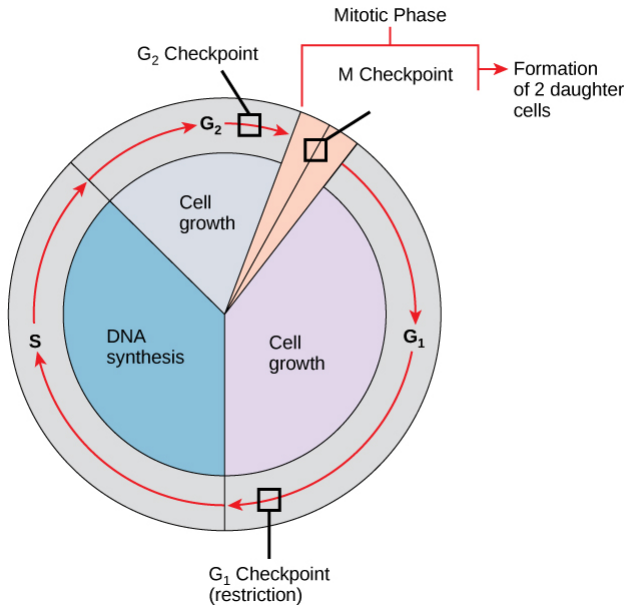
The length of the cell cycle is highly variable even within the cells of an individual organism. In humans, the frequency of cell turnover ranges from a few hours in early embryonic development to an average of two to five days for epithelial cells, or to an entire human lifetime spent in G_0 by specialized cells such as cortical neurons or cardiac muscle cells. There is also variation in the time that a cell

spends in each phase of the cell cycle. When fast-dividing mammalian cells are grown in culture (outside the body under optimal growing conditions), the length of the cycle is approximately 24 hours. In rapidly dividing human cells with a 24-hour cell cycle, the G₁ phase lasts approximately 11 hours. The timing of events in the cell cycle is controlled by mechanisms that are both internal and external to the cell.

The cell cycle is controlled at three checkpoints. Integrity of the DNA is assessed at the G₁ checkpoint. Proper chromosome duplication is assessed at the G₂ checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at the M checkpoint.

Regulation at Internal Checkpoints

It is essential that daughter cells be exact duplicates of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from the abnormal cell. To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main **cell cycle checkpoints** at which the cell cycle can be stopped until conditions are favorable. These checkpoints occur near the end of G₁, at the G₂–M transition, and during metaphase ([\[link\]](#)).



The G₁ Checkpoint

The G₁ checkpoint determines whether all conditions are favorable for cell division to proceed. The G₁ checkpoint, also called the restriction point, is the point at which the cell irreversibly commits to the cell-division process. In addition to adequate reserves and cell size, there is a check for damage to the genomic DNA at the G₁ checkpoint. A cell that does not meet all the requirements will not be released into the S phase.

The G₂ Checkpoint

The G₂ checkpoint bars the entry to the mitotic phase if certain conditions are not met. As in the G₁

checkpoint, cell size and protein reserves are assessed. However, the most important role of the G₂ checkpoint is to ensure that all of the chromosomes have been replicated and that the replicated DNA is not damaged.

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of mitosis. The M checkpoint is also known as the spindle checkpoint because it determines if all the sister chromatids are correctly attached to the spindle microtubules. Because the separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until the kinetochores of each pair of sister chromatids are firmly anchored to spindle fibers arising from opposite poles of the cell.

Concept in Action



Watch what occurs at the G₁, G₂, and M

checkpoints by visiting [this animation](#) of the cell cycle.

Section Summary

The cell cycle is an orderly sequence of events. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages. In eukaryotes, the cell cycle consists of a long preparatory period, called interphase. Interphase is divided into G₁, S, and G₂ phases. Mitosis consists of five stages: prophase, prometaphase, metaphase, anaphase, and telophase. Mitosis is usually accompanied by cytokinesis, during which the cytoplasmic components of the daughter cells are separated either by an actin ring (animal cells) or by cell plate formation (plant cells).

Each step of the cell cycle is monitored by internal controls called checkpoints. There are three major checkpoints in the cell cycle: one near the end of G₁, a second at the G₂–M transition, and the third during metaphase.

Art Connections

[\[link\]](#) Which of the following is the correct order of events in mitosis?

1. Sister chromatids line up at the metaphase plate. The kinetochore becomes attached to the mitotic spindle. The nucleus re-forms and the cell divides. The sister chromatids separate.
2. The kinetochore becomes attached to the mitotic spindle. The sister chromatids separate. Sister chromatids line up at the metaphase plate. The nucleus re-forms and the cell divides.
3. The kinetochore becomes attached to metaphase plate. Sister chromatids line up at the metaphase plate. The kinetochore breaks down and the sister chromatids separate. The nucleus re-forms and the cell divides.
4. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks apart and the sister chromatids separate. The nucleus re-forms and the cell divides.

[\[link\]](#) D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks

apart and the sister chromatids separate. The nucleus reforms and the cell divides.

Multiple Choice

Chromosomes are duplicated during what portion of the cell cycle?

1. G₁ phase
2. S phase
3. prophase
4. prometaphase

B

Separation of the sister chromatids is a characteristic of which stage of mitosis?

1. prometaphase
2. metaphase
3. anaphase
4. telophase

C

The individual chromosomes become visible with a light microscope during which stage of mitosis?

1. prophase
 2. prometaphase
 3. metaphase
 4. anaphase
-

A

What is necessary for a cell to pass the G₂ checkpoint?

1. cell has reached a sufficient size
 2. an adequate stockpile of nucleotides
 3. accurate and complete DNA replication
 4. proper attachment of mitotic spindle fibers to kinetochores
-

C

Free Response

Describe the similarities and differences

between the cytokinesis mechanisms found in animal cells versus those in plant cells.

There are very few similarities between animal cell and plant cell cytokinesis. In animal cells, a ring of actin fibers is formed around the periphery of the cell at the former metaphase plate. The actin ring contracts inward, pulling the plasma membrane toward the center of the cell until the cell is pinched in two. In plant cells, a new cell wall must be formed between the daughter cells. Because of the rigid cell walls of the parent cell, contraction of the middle of the cell is not possible. Instead, a cell plate is formed in the center of the cell at the former metaphase plate. The cell plate is formed from Golgi vesicles that contain enzymes, proteins, and glucose. The vesicles fuse and the enzymes build a new cell wall from the proteins and glucose. The cell plate grows toward, and eventually fuses with, the cell wall of the parent cell.

Glossary

anaphase

the stage of mitosis during which sister chromatids are separated from each other

cell cycle

the ordered sequence of events that a cell passes through between one cell division and the next

cell cycle checkpoints

mechanisms that monitor the preparedness of a eukaryotic cell to advance through the various cell cycle stages

cell plate

a structure formed during plant-cell cytokinesis by Golgi vesicles fusing at the metaphase plate; will ultimately lead to formation of a cell wall to separate the two daughter cells

centriole

a paired rod-like structure constructed of microtubules at the center of each animal cell centrosome

cleavage furrow

a constriction formed by the actin ring during animal-cell cytokinesis that leads to cytoplasmic division

cytokinesis

the division of the cytoplasm following mitosis to form two daughter cells

G₀ phase

a cell-cycle phase distinct from the G₁ phase

of interphase; a cell in G₀ is not preparing to divide

G₁ phase

(also, first gap) a cell-cycle phase; first phase of interphase centered on cell growth during mitosis

G₂ phase

(also, second gap) a cell-cycle phase; third phase of interphase where the cell undergoes the final preparations for mitosis

interphase

the period of the cell cycle leading up to mitosis; includes G₁, S, and G₂ phases; the interim between two consecutive cell divisions

kinetochore

a protein structure in the centromere of each sister chromatid that attracts and binds spindle microtubules during prometaphase

metaphase plate

the equatorial plane midway between two poles of a cell where the chromosomes align during metaphase

metaphase

the stage of mitosis during which chromosomes are lined up at the metaphase

plate

mitosis

the period of the cell cycle at which the duplicated chromosomes are separated into identical nuclei; includes prophase, prometaphase, metaphase, anaphase, and telophase

mitotic phase

the period of the cell cycle when duplicated chromosomes are distributed into two nuclei and the cytoplasmic contents are divided; includes mitosis and cytokinesis

mitotic spindle

the microtubule apparatus that orchestrates the movement of chromosomes during mitosis

prometaphase

the stage of mitosis during which mitotic spindle fibers attach to kinetochores

prophase

the stage of mitosis during which chromosomes condense and the mitotic spindle begins to form

quiescent

describes a cell that is performing normal cell functions and has not initiated preparations for cell division

S phase

the second, or synthesis phase, of interphase during which DNA replication occurs

telophase

the stage of mitosis during which chromosomes arrive at opposite poles, decondense, and are surrounded by new nuclear envelopes

Meiosis

By the end of this section, you will be able to:

- Describe the behavior of chromosomes during meiosis
- Describe cellular events during meiosis
- Explain the differences between meiosis and mitosis
- Explain the mechanisms within meiosis that generate genetic variation among the products of meiosis

Sexual reproduction requires **fertilization**, a union of two cells from two individual organisms. If those two cells each contain one set of chromosomes, then the resulting cell contains two sets of chromosomes. The number of sets of chromosomes in a cell is called its ploidy level. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. If the reproductive cycle is to continue, the diploid cell must somehow reduce its number of chromosome sets before fertilization can occur again, or there will be a continual doubling in the number of chromosome sets in every generation. So, in addition to fertilization, sexual reproduction includes a nuclear division, known as meiosis, that reduces the number of chromosome sets.

Most animals and plants are diploid, containing two sets of chromosomes; in each **somatic cell** (the

nonreproductive cells of a multicellular organism), the nucleus contains two copies of each chromosome that are referred to as homologous chromosomes. Somatic cells are sometimes referred to as “body” cells. Homologous chromosomes are matched pairs containing genes for the same traits in identical locations along their length. Diploid organisms inherit one copy of each homologous chromosome from each parent; all together, they are considered a full set of chromosomes. In animals, haploid cells containing a single copy of each homologous chromosome are found only within gametes. Gametes fuse with another haploid gamete to produce a diploid cell.

The nuclear division that forms haploid cells, which is called meiosis, is related to mitosis. As you have learned, mitosis is part of a cell reproduction cycle that results in identical daughter nuclei that are also genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei contain the same number of chromosome sets—diploid for most plants and animals. Meiosis employs many of the same mechanisms as mitosis. However, the starting nucleus is always diploid and the nuclei that result at the end of a meiotic cell division are haploid. To achieve the reduction in chromosome number, meiosis consists of one round of chromosome duplication and two rounds of nuclear division. Because the events that occur during each of the division stages are analogous to

the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the stages are designated with a “I” or “II.” Thus, **meiosis I** is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Meiosis I reduces the number of chromosome sets from two to one. The genetic information is also mixed during this division to create unique recombinant chromosomes. **Meiosis II**, in which the second round of meiotic division takes place in a way that is similar to mitosis, includes prophase II, prometaphase II, and so on.

Interphase

Meiosis is preceded by an interphase consisting of the G₁, S, and G₂ phases, which are nearly identical to the phases preceding mitosis. The G₁ phase is the first phase of interphase and is focused on cell growth. In the S phase, the DNA of the chromosomes is replicated. Finally, in the G₂ phase, the cell undergoes the final preparations for meiosis.

During DNA duplication of the S phase, each chromosome becomes composed of two identical copies (called sister chromatids) that are held together at the centromere until they are pulled apart during meiosis II. In an animal cell, the centrosomes that organize the microtubules of the meiotic spindle also replicate. This prepares the cell

for the first meiotic phase.

In this illustration of the effects of crossing over, the blue chromosome came from the individual's father and the red chromosome came from the individual's mother. Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes. The chromosomes that have a mixture of maternal and paternal sequence are called recombinant and the chromosomes that are completely paternal or maternal are called non-recombinant. To demonstrate random, independent assortment at metaphase I, consider a cell with $n = 2$. In this case, there are two possible arrangements at the equatorial plane in metaphase I, as shown in the upper cell of each panel. These two possible orientations lead to the production of genetically different gametes. With more chromosomes, the number of possible arrangements increases dramatically.

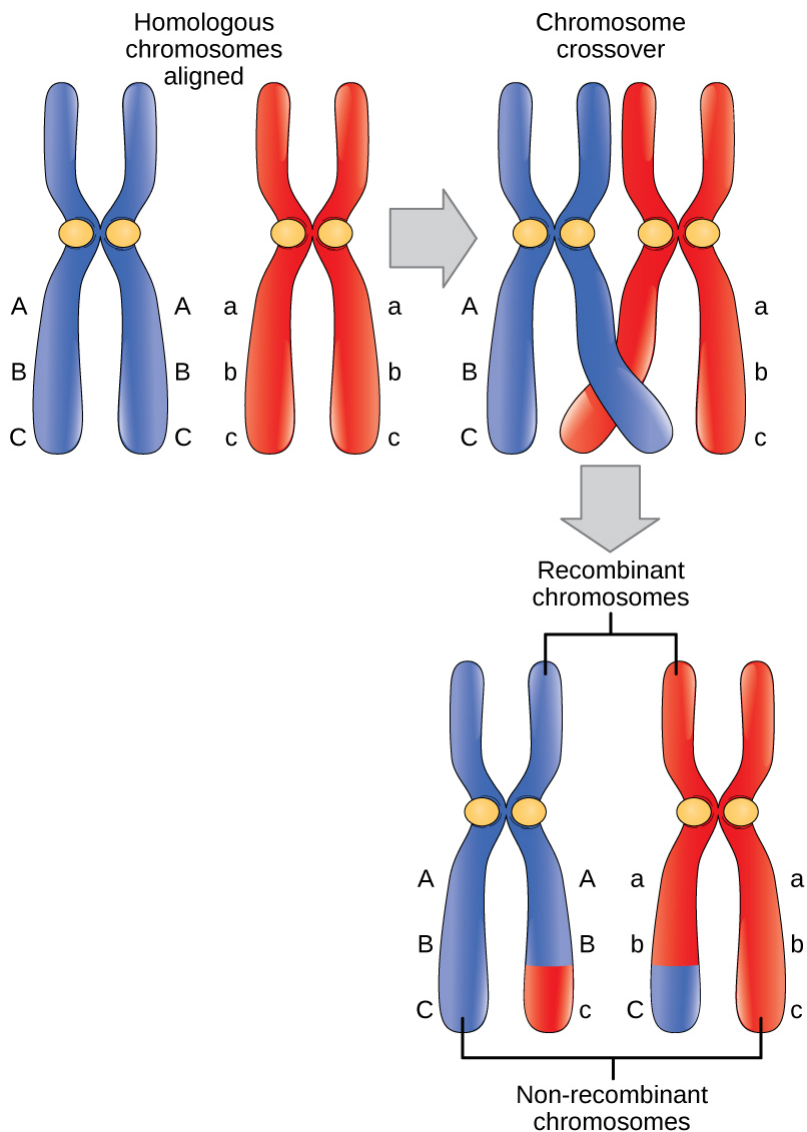
Meiosis I

Early in prophase I, the chromosomes can be seen clearly microscopically. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair close to each other. The tight pairing of the homologous chromosomes is called **synapsis**. In synapsis, the genes on the chromatids of the homologous chromosomes are precisely aligned with each other.

An exchange of chromosome segments between non-sister homologous chromatids occurs and is called **crossing over**. This process is revealed visually after the exchange as **chiasmata** (singular = *chiasma*) ([\[link\]](#)).

As prophase I progresses, the close association between homologous chromosomes begins to break down, and the chromosomes continue to condense, although the homologous chromosomes remain attached to each other at chiasmata. The number of chiasmata varies with the species and the length of the chromosome. At the end of prophase I, the pairs are held together only at chiasmata ([\[link\]](#)) and are called **tetrads** because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete, it will carry some DNA from one parent of the individual and some DNA from the other parent. The **recombinant** sister chromatid has a combination of maternal and paternal genes that did not exist before the crossover.



The key event in prometaphase I is the attachment of the spindle fiber microtubules to the kinetochore proteins at the centromeres. The microtubules assembled from centrosomes at opposite poles of the cell grow toward the middle of the cell. At the end

of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome attached at one pole and the other homologous chromosome attached to the other pole. The homologous chromosomes are still held together at chiasmata. In addition, the nuclear membrane has broken down entirely.

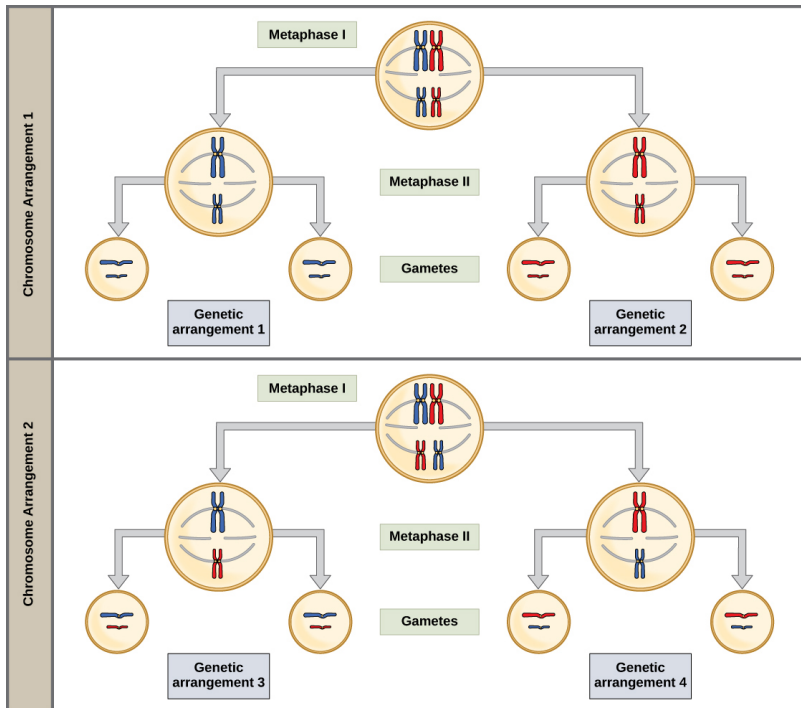
During metaphase I, the homologous chromosomes are arranged in the center of the cell with the kinetochores facing opposite poles. The orientation of each pair of homologous chromosomes at the center of the cell is random.

This randomness, called independent assortment, is the physical basis for the generation of the second form of genetic variation in offspring. Consider that the homologous chromosomes of a sexually reproducing organism are originally inherited as two separate sets, one from each parent. Using humans as an example, one set of 23 chromosomes is present in the egg donated by the mother. The father provides the other set of 23 chromosomes in the sperm that fertilizes the egg. In metaphase I, these pairs line up at the midway point between the two poles of the cell. Because there is an equal chance that a microtubule fiber will encounter a maternally or paternally inherited chromosome, the arrangement of the tetrads at the metaphase plate is random. Any maternally inherited chromosome may face either pole. Any paternally inherited

chromosome may also face either pole. The orientation of each tetrad is independent of the orientation of the other 22 tetrads.

In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations depends on the number of chromosomes making up a set. There are two possibilities for orientation (for each tetrad); thus, the possible number of alignments equals 2^n where n is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possibilities. This number does not include the variability previously created in the sister chromatids by crossover. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition ([\[link\]](#)).

To summarize the genetic consequences of meiosis I: the maternal and paternal genes are recombined by crossover events occurring on each homologous pair during prophase I; in addition, the random assortment of tetrads at metaphase produces a unique combination of maternal and paternal chromosomes that will make their way into the gametes.



In anaphase I, the spindle fibers pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. It is the chiasma connections that are broken in anaphase I as the fibers attached to the fused kinetochores pull the homologous chromosomes apart ([\[link\]](#)).

In telophase I, the separated chromosomes arrive at opposite poles. The remainder of the typical telophase events may or may not occur depending on the species. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I.

Cytokinesis, the physical separation of the

cytoplasmic components into two daughter cells, occurs without reformation of the nuclei in other organisms. In nearly all species, cytokinesis separates the cell contents by either a cleavage furrow (in animals and some fungi), or a cell plate that will ultimately lead to formation of cell walls that separate the two daughter cells (in plants). At each pole, there is just one member of each pair of the homologous chromosomes, so only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, even though there are duplicate copies of the set because each homolog still consists of two sister chromatids that are still attached to each other. However, although the sister chromatids were once duplicates of the same chromosome, they are no longer identical at this stage because of crossovers.

Concept in Action



Review the process of meiosis, observing how

chromosomes align and migrate, at [this site](#).

In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to individual kinetochores of sister chromatids. In anaphase II, the sister chromatids are separated.

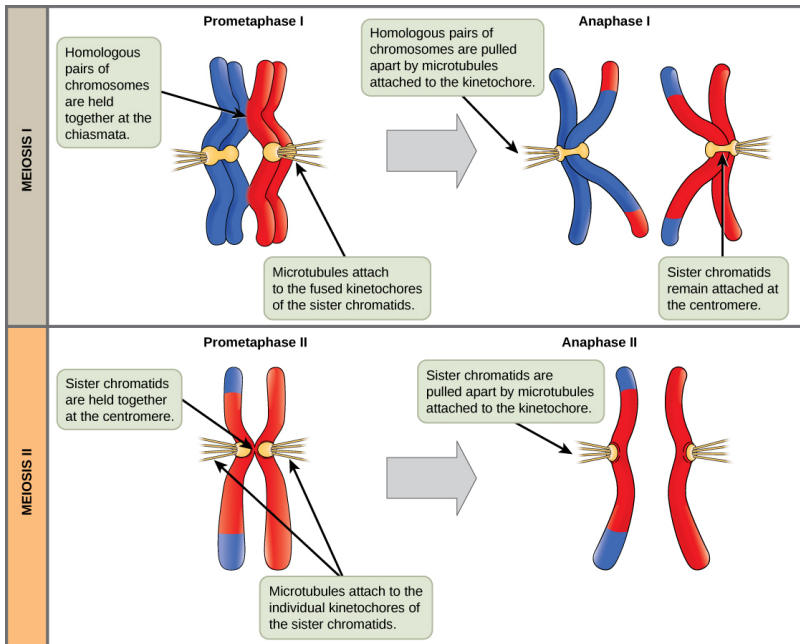
Meiosis II

In meiosis II, the connected sister chromatids remaining in the haploid cells from meiosis I will be split to form four haploid cells. In some species, cells enter a brief interphase, or **interkinesis**, that lacks an S phase, before entering meiosis II.

Chromosomes are not duplicated during interkinesis. The two cells produced in meiosis I go through the events of meiosis II in synchrony. Overall, meiosis II resembles the mitotic division of a haploid cell.

In prophase II, if the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes duplicated during interkinesis move away from each other toward opposite poles, and new spindles are formed. In prometaphase II, the nuclear envelopes are completely broken down,

and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles. In metaphase II, the sister chromatids are maximally condensed and aligned at the center of the cell. In anaphase II, the sister chromatids are pulled apart by the spindle fibers and move toward opposite poles.



In telophase II, the chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four genetically unique haploid cells. At this point, the nuclei in the newly produced cells are both haploid and have only one copy of the single set of chromosomes. The cells produced are genetically unique because of the

random assortment of paternal and maternal homologs and because of the recombination of maternal and paternal segments of chromosomes—with their sets of genes—that occurs during crossover.

Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

Comparing Meiosis and Mitosis

Mitosis and meiosis, which are both forms of division of the nucleus in eukaryotic cells, share some similarities, but also exhibit distinct differences that lead to their very different outcomes. Mitosis is a single nuclear division that results in two nuclei, usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original. They have the same number of sets of chromosomes: one in the case of haploid cells, and two in the case of diploid cells. On the other hand, meiosis is two nuclear divisions that result in four nuclei, usually partitioned into four new cells. The nuclei resulting from meiosis are never genetically identical, and they contain one chromosome set only—this is half the number of the original cell, which was diploid ([link]).

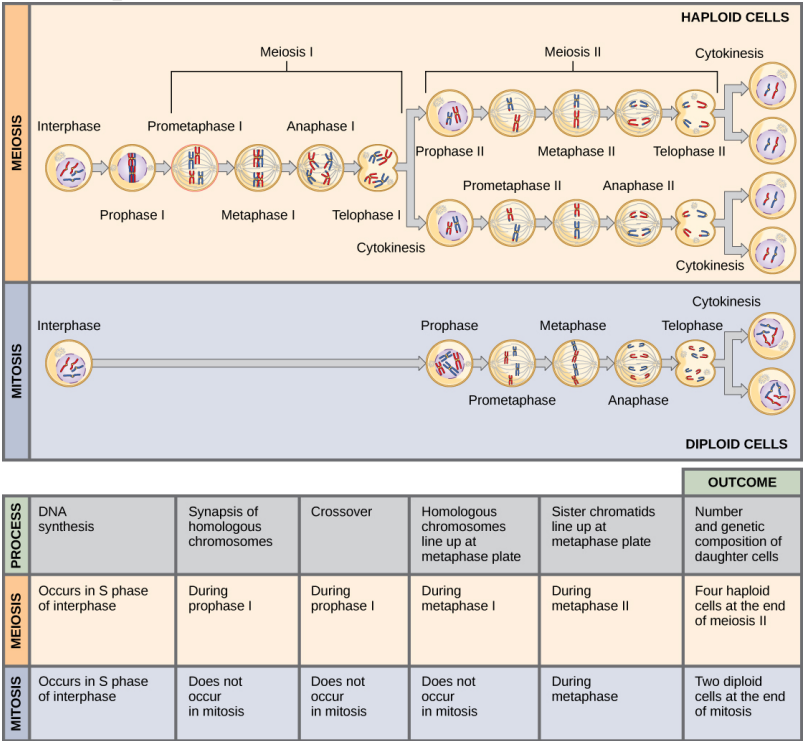
The differences in the outcomes of meiosis and mitosis occur because of differences in the behavior of the chromosomes during each process. Most of these differences in the processes occur in meiosis I, which is a very different nuclear division than mitosis. In meiosis I, the homologous chromosome pairs become associated with each other, are bound together, experience chiasmata and crossover between sister chromatids, and line up along the metaphase plate in tetrads with spindle fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I, never in mitosis.

Homologous chromosomes move to opposite poles during meiosis I so the number of sets of chromosomes in each nucleus-to-be is reduced from two to one. For this reason, meiosis I is referred to as a **reduction division**. There is no such reduction in ploidy level in mitosis.

Meiosis II is much more analogous to a mitotic division. In this case, duplicated chromosomes (only one set of them) line up at the center of the cell with divided kinetochores attached to spindle fibers from opposite poles. During anaphase II, as in mitotic anaphase, the kinetochores divide and one sister chromatid is pulled to one pole and the other sister chromatid is pulled to the other pole. If it were not for the fact that there had been crossovers, the two products of each meiosis II division would

be identical as in mitosis; instead, they are different because there has always been at least one crossover per chromosome. Meiosis II is not a reduction division because, although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I.

Cells produced by mitosis will function in different parts of the body as a part of growth or replacing dead or damaged cells. They may even be involved in asexual reproduction in some organisms. Cells produced by meiosis in a diploid-dominant organism such as an animal will only participate in sexual reproduction.



Concept in Action



For an animation comparing mitosis and meiosis, go to [this website](#).

Section Summary

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. The process that results in haploid cells is called meiosis. Meiosis is a series of events that arrange and separate chromosomes into daughter cells. During the interphase of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four haploid daughter cells, each with half the number of chromosomes as the parent cell. During meiosis, variation in the daughter nuclei is

introduced because of crossover in prophase I and random alignment at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similarities, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce daughter nuclei that are genetically identical and have the same number of chromosome sets as the original cell. Meiotic divisions are two nuclear divisions that produce four daughter nuclei that are genetically different and have one chromosome set rather than the two sets the parent cell had. The main differences between the processes occur in the first division of meiosis. The homologous chromosomes separate into different nuclei during meiosis I causing a reduction of ploidy level. The second division of meiosis is much more similar to a mitotic division.

Multiple Choice

Meiosis produces _____ daughter cells.

1. two haploid
 2. two diploid
 3. four haploid
 4. four diploid
-

C

At which stage of meiosis are sister chromatids separated from each other?

1. prophase I
2. prophase II
3. anaphase I
4. anaphase II

D

The part of meiosis that is similar to mitosis is _____.

1. meiosis I
2. anaphase I
3. meiosis II
4. interkinesis

C

If a muscle cell of a typical organism has 32 chromosomes, how many chromosomes will be in a gamete of that same organism?

1. 8

2. 16
3. 32
4. 64

B

Free Response

Explain how the random alignment of homologous chromosomes during metaphase I contributes to variation in gametes produced by meiosis.

Random alignment leads to new combinations of traits. The chromosomes that were originally inherited by the gamete-producing individual came equally from the egg and the sperm. In metaphase I, the duplicated copies of these maternal and paternal homologous chromosomes line up across the center of the cell to form a tetrad. The orientation of each tetrad is random. There is an equal chance that the maternally derived chromosomes will be facing either pole. The same is true of the paternally derived chromosomes. The alignment should occur differently in almost

every meiosis. As the homologous chromosomes are pulled apart in anaphase I, any combination of maternal and paternal chromosomes will move toward each pole. The gametes formed from these two groups of chromosomes will have a mixture of traits from the individual's parents. Each gamete is unique.

In what ways is meiosis II similar to and different from mitosis of a diploid cell?

The two divisions are similar in that the chromosomes line up along the metaphase plate individually, meaning unpaired with other chromosomes (as in meiosis I). In addition, each chromosome consists of two sister chromatids that will be pulled apart. The two divisions are different because in meiosis II there are half the number of chromosomes that are present in a diploid cell of the same species undergoing mitosis. This is because meiosis I reduced the number of chromosomes to a haploid state.

Glossary

chiasmata

(singular = *chiasma*) the structure that forms at the crossover points after genetic material

is exchanged

crossing over

(also, recombination) the exchange of genetic material between homologous chromosomes resulting in chromosomes that incorporate genes from both parents of the organism forming reproductive cells

fertilization

the union of two haploid cells typically from two individual organisms

interkinesis

a period of rest that may occur between meiosis I and meiosis II; there is no replication of DNA during interkinesis

meiosis I

the first round of meiotic cell division; referred to as reduction division because the resulting cells are haploid

meiosis II

the second round of meiotic cell division following meiosis I; sister chromatids are separated from each other, and the result is four unique haploid cells

recombinant

describing something composed of genetic material from two sources, such as a

chromosome with both maternal and paternal segments of DNA

reduction division

a nuclear division that produces daughter nuclei each having one-half as many chromosome sets as the parental nucleus; meiosis I is a reduction division

somatic cell

all the cells of a multicellular organism except the gamete-forming cells

synapsis

the formation of a close association between homologous chromosomes during prophase I

tetrad

two duplicated homologous chromosomes (four chromatids) bound together by chiasmata during prophase I

Transcription

By the end of this section, you will be able to:

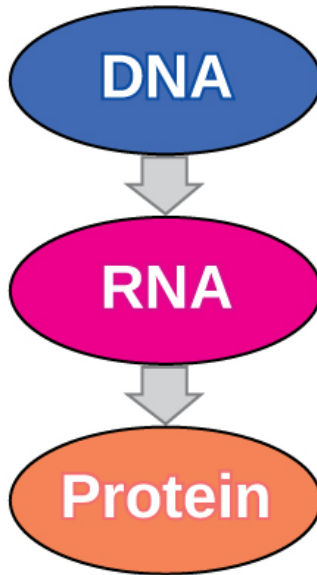
- Explain the central dogma
- Explain the main steps of transcription
- Describe how eukaryotic mRNA is processed

In both prokaryotes and eukaryotes, the second function of DNA (the first was replication) is to provide the information needed to construct the proteins necessary so that the cell can perform all of its functions. To do this, the DNA is “read” or transcribed into an **mRNA** molecule. The mRNA then provides the code to form a protein by a process called translation. Through the processes of transcription and translation, a protein is built with a specific sequence of amino acids that was originally encoded in the DNA. This module discusses the details of transcription.

The central dogma states that DNA encodes RNA, which in turn encodes protein.

The Central Dogma: DNA Encodes RNA; RNA Encodes Protein

The flow of genetic information in cells from DNA to mRNA to protein is described by the central dogma ([\[link\]](#)), which states that genes specify the sequences of mRNAs, which in turn specify the sequences of proteins.



The copying of DNA to mRNA is relatively straightforward, with one nucleotide being added to the mRNA strand for every complementary nucleotide read in the DNA strand. The translation to protein is more complex because groups of three mRNA nucleotides correspond to one amino acid of the protein sequence. However, as we shall see in the next module, the translation to protein is still systematic, such that nucleotides 1 to 3 correspond to amino acid 1, nucleotides 4 to 6 correspond to amino acid 2, and so on.

The initiation of transcription begins when DNA is unwound, forming a transcription bubble. Enzymes and other proteins involved in transcription bind at the promoter. During elongation, RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds then rewinds

the DNA as it is read. Multiple polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. In this way, a specific protein can rapidly reach a high concentration in the bacterial cell.

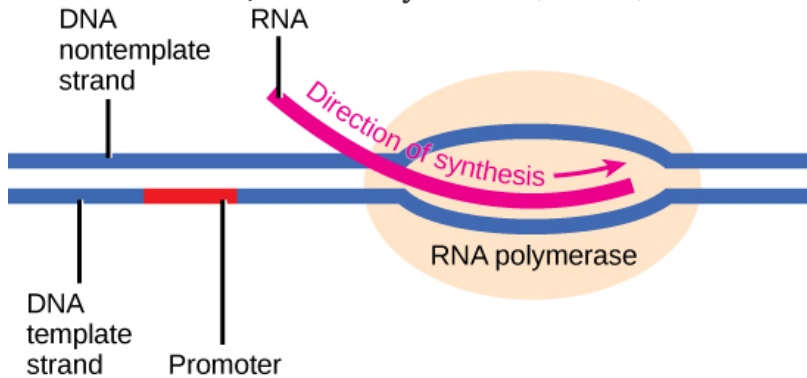
Transcription: from DNA to mRNA

Both prokaryotes and eukaryotes perform fundamentally the same process of transcription, with the important difference of the membrane-bound nucleus in eukaryotes. With the genes bound in the nucleus, transcription occurs in the nucleus of the cell and the mRNA transcript must be transported to the cytoplasm. The prokaryotes, which include bacteria and archaea, lack membrane-bound nuclei and other organelles, and transcription occurs in the cytoplasm of the cell. In both prokaryotes and eukaryotes, transcription occurs in three main stages: initiation, elongation, and termination.

Initiation

Transcription requires the DNA double helix to partially unwind in the region of mRNA synthesis. The region of unwinding is called a **transcription bubble**. The DNA sequence onto which the proteins and enzymes involved in transcription bind to

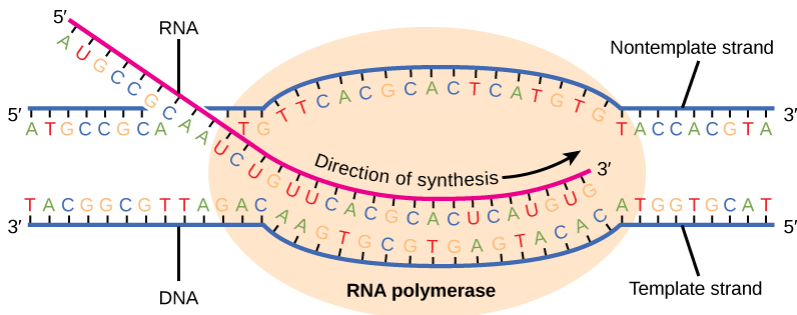
initiate the process is called a **promoter**. In most cases, promoters exist upstream of the genes they regulate. The specific sequence of a promoter is very important because it determines whether the corresponding gene is transcribed all of the time, some of the time, or hardly at all ([\[link\]](#)).



Elongation

Transcription always proceeds from one of the two DNA strands, which is called the **template strand**. The mRNA product is complementary to the template strand and is almost identical to the other DNA strand, called the **nontemplate strand**, with the exception that RNA contains a uracil (U) in place of the thymine (T) found in DNA. During elongation, an enzyme called **RNA polymerase** proceeds along the DNA template adding nucleotides by base pairing with the DNA template in a manner similar to DNA replication, with the difference that an RNA strand is being synthesized that does not remain bound to the DNA template. As elongation proceeds, the DNA is continuously

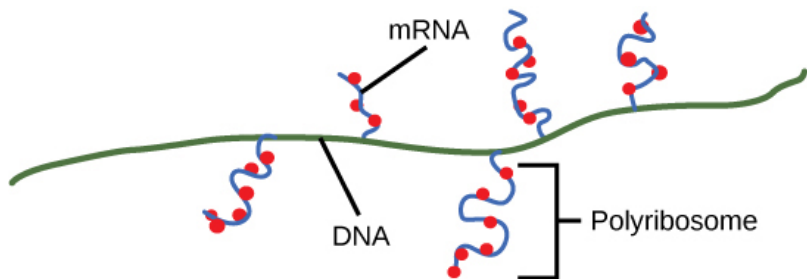
unwound ahead of the core enzyme and rewind behind it ([link]).



Termination

Once a gene is transcribed, the prokaryotic polymerase needs to be instructed to dissociate from the DNA template and liberate the newly made mRNA. Depending on the gene being transcribed, there are two kinds of termination signals, but both involve repeated nucleotide sequences in the DNA template that result in RNA polymerase stalling, leaving the DNA template, and freeing the mRNA transcript.

On termination, the process of transcription is complete. In a prokaryotic cell, by the time termination occurs, the transcript would already have been used to partially synthesize numerous copies of the encoded protein because these processes can occur concurrently using multiple ribosomes (polyribosomes) ([link]). In contrast, the presence of a nucleus in eukaryotic cells precludes simultaneous transcription and translation.



Eukaryotic mRNA contains introns that must be spliced out. A 5' cap and 3' tail are also added.

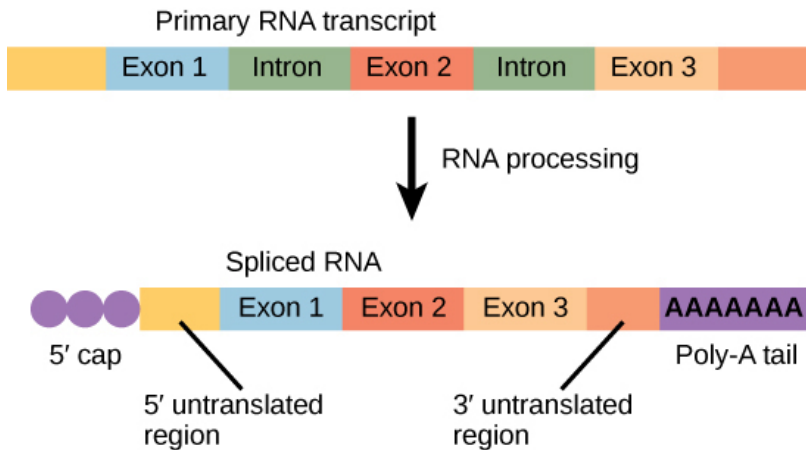
Eukaryotic RNA Processing

The newly transcribed eukaryotic mRNAs must undergo several processing steps before they can be transferred from the nucleus to the cytoplasm and translated into a protein. The additional steps involved in eukaryotic mRNA maturation create a molecule that is much more stable than a prokaryotic mRNA. For example, eukaryotic mRNAs last for several hours, whereas the typical prokaryotic mRNA lasts no more than five seconds.

The mRNA transcript is first coated in RNA-stabilizing proteins to prevent it from degrading while it is processed and exported out of the nucleus. This occurs while the pre-mRNA still is being synthesized by adding a special nucleotide “cap” to the 5' end of the growing transcript. In addition to preventing degradation, factors involved in protein synthesis recognize the cap to help initiate translation by ribosomes.

Once elongation is complete, an enzyme then adds a string of approximately 200 adenine residues to the 3' end, called the poly-A tail. This modification further protects the pre-mRNA from degradation and signals to cellular factors that the transcript needs to be exported to the cytoplasm.

Eukaryotic genes are composed of protein-coding sequences called **exons** (*ex-on* signifies that they are *expressed*) and *intervening* sequences called **introns** (*int-ron* denotes their *intervening* role). Introns are removed from the pre-mRNA during processing. Intron sequences in mRNA do not encode functional proteins. It is essential that all of a pre-mRNA's introns be completely and precisely removed before protein synthesis so that the exons join together to code for the correct amino acids. If the process errs by even a single nucleotide, the sequence of the rejoined exons would be shifted, and the resulting protein would be nonfunctional. The process of removing introns and reconnecting exons is called **splicing** ([\[link\]](#)). Introns are removed and degraded while the pre-mRNA is still in the nucleus.



Section Summary

In prokaryotes, mRNA synthesis is initiated at a promoter sequence on the DNA template. Elongation synthesizes new mRNA. Termination liberates the mRNA and occurs by mechanisms that stall the RNA polymerase and cause it to fall off the DNA template. Newly transcribed eukaryotic mRNAs are modified with a cap and a poly-A tail. These structures protect the mature mRNA from degradation and help export it from the nucleus. Eukaryotic mRNAs also undergo splicing, in which introns are removed and exons are reconnected with single-nucleotide accuracy. Only finished mRNAs are exported from the nucleus to the cytoplasm.

Multiple Choice

A promoter is _____.

1. a specific sequence of DNA nucleotides
 2. a specific sequence of RNA nucleotides
 3. a protein that binds to DNA
 4. an enzyme that synthesizes RNA
-

A

Portions of eukaryotic mRNA sequence that are removed during RNA processing are _____.

1. exons
 2. caps
 3. poly-A tails
 4. introns
-

D

Glossary

exon

a sequence present in protein-coding mRNA
after completion of pre-mRNA splicing

intron

non-protein-coding intervening sequences

that are spliced from mRNA during processing

mRNA

messenger RNA; a form of RNA that carries the nucleotide sequence code for a protein sequence that is translated into a polypeptide sequence

nontemplate strand

the strand of DNA that is not used to transcribe mRNA; this strand is identical to the mRNA except that T nucleotides in the DNA are replaced by U nucleotides in the mRNA

promoter

a sequence on DNA to which RNA polymerase and associated factors bind and initiate transcription

RNA polymerase

an enzyme that synthesizes an RNA strand from a DNA template strand

splicing

the process of removing introns and reconnecting exons in a pre-mRNA

template strand

the strand of DNA that specifies the complementary mRNA molecule

transcription bubble

the region of locally unwound DNA that
allows for transcription of mRNA

Translation

By the end of this section, you will be able to:

- Describe the different steps in protein synthesis
- Discuss the role of ribosomes in protein synthesis
- Describe the genetic code and how the nucleotide sequence determines the amino acid and the protein sequence

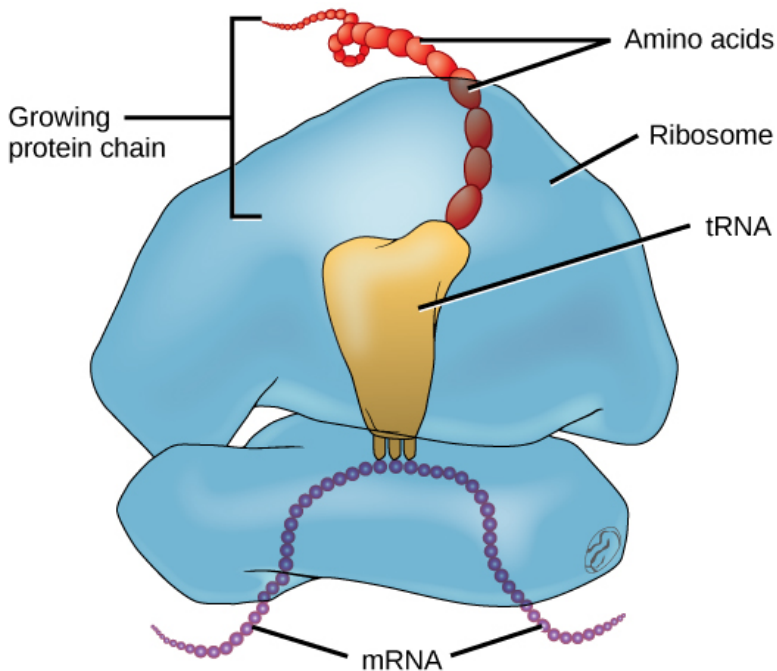
The synthesis of proteins is one of a cell's most energy-consuming metabolic processes. In turn, proteins account for more mass than any other component of living organisms (with the exception of water), and proteins perform a wide variety of the functions of a cell. The process of translation, or protein synthesis, involves decoding an mRNA message into a polypeptide product. Amino acids are covalently strung together in lengths ranging from approximately 50 amino acids to more than 1,000.

The protein synthesis machinery includes the large and small subunits of the ribosome, mRNA, and tRNA. (credit: modification of work by NIGMS, NIH)

The Protein Synthesis Machinery

In addition to the mRNA template, many other molecules contribute to the process of translation. The composition of each component may vary

across species; for instance, ribosomes may consist of different numbers of ribosomal RNAs (**rRNA**) and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors ([\[link\]](#)).



In *E. coli*, there are 200,000 ribosomes present in every cell at any given time. A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the nucleolus is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes are located in the cytoplasm in prokaryotes and in the cytoplasm and endoplasmic reticulum of eukaryotes. Ribosomes are made up of a large and a small subunit that come together for translation. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds **tRNAs**, a type of RNA molecule that brings amino acids to the growing chain of the polypeptide. Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction.

Depending on the species, 40 to 60 types of tRNA exist in the cytoplasm. Serving as adaptors, specific tRNAs bind to sequences on the mRNA template and add the corresponding amino acid to the polypeptide chain. Therefore, tRNAs are the molecules that actually “translate” the language of RNA into the language of proteins. For each tRNA to function, it must have its specific amino acid bonded to it. In the process of tRNA “charging,” each tRNA molecule is bonded to its correct amino acid.

This figure shows the genetic code for translating each nucleotide triplet, or codon, in mRNA into an amino acid or a termination signal in a nascent protein. (credit: modification of work by NIH)

The Genetic Code

To summarize what we know to this point, the

cellular process of transcription generates messenger RNA (mRNA), a mobile molecular copy of one or more genes with an alphabet of A, C, G, and uracil (U). Translation of the mRNA template converts nucleotide-based genetic information into a protein product. Protein sequences consist of 20 commonly occurring amino acids; therefore, it can be said that the protein alphabet consists of 20 letters. Each amino acid is defined by a three-nucleotide sequence called the triplet **codon**. The relationship between a nucleotide codon and its corresponding amino acid is called the **genetic code**.

Given the different numbers of “letters” in the mRNA and protein “alphabets,” combinations of nucleotides corresponded to single amino acids. Using a three-nucleotide code means that there are a total of 64 ($4 \times 4 \times 4$) possible combinations; therefore, a given amino acid is encoded by more than one nucleotide triplet ([\[link\]](#)).

		Second letter					
		U	C	A	G		
First letter	U	UUU } Phe UUC } UUA } Leu UUG }	UCU } UCC } Ser UCA } UCG }	UAU } Tyr UAC } UAA Stop UAG Stop	UGU } Cys UGC } UGA Stop UGG Trp	U C A G	Third letter
	C	CUU } CUC } Leu CUA } CUG }	CCU } CCC } Pro CCA } CCG }	CAU } His CAC } CAA } Gln CAG }	CGU } CGC } Arg CGA } CGG }	U C A G	
	A	AUU } AUC } Ile AUA } AUG Met	ACU } ACC } Thr ACA } ACG }	AAU } Asn AAC } AAA } Lys AAG }	AGU } Ser AGC } AGA } Arg AGG }	U C A G	
	G	GUU } GUC } Val GUA } GUG }	GCU } GCC } Ala GCA } GCG }	GAU } Asp GAC } GAA } Glu GAG }	GGU } GGC } Gly GGA } GGG }	U C A G	

Three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called **stop codons**. Another codon, AUG, also has a special function. In addition to specifying the amino acid methionine, it also serves as the **start codon** to initiate translation. The reading frame for translation is set by the AUG start codon near the 5' end of the mRNA. The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis, which is powerful evidence that all life on Earth shares a common origin.

Translation begins when a tRNA anticodon recognizes a codon on the mRNA. The large ribosomal subunit joins the small subunit, and a

second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. Entry of a release factor into the A site terminates translation and the components dissociate.

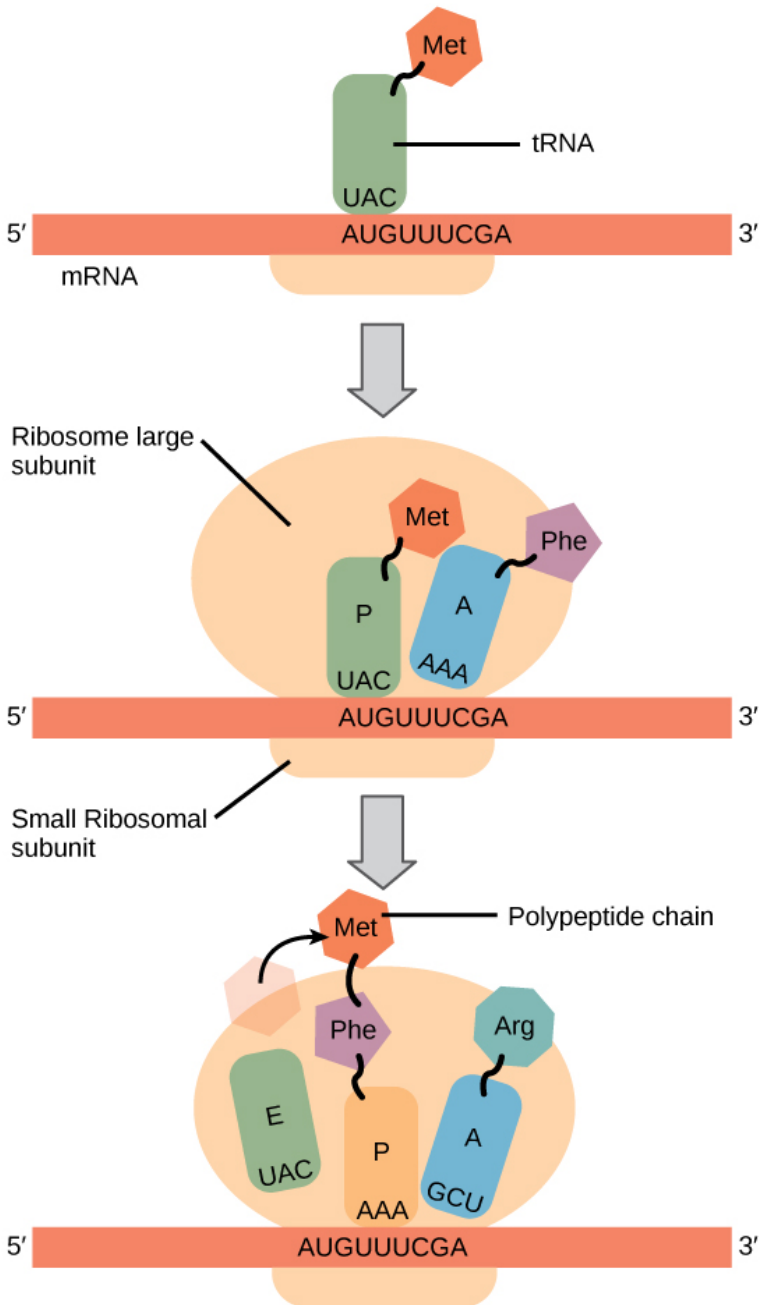
The Mechanism of Protein Synthesis

Just as with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination. The process of translation is similar in prokaryotes and eukaryotes. Here we will explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between prokaryotic and eukaryotic translation.

Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small ribosome subunit, the mRNA template, three initiation factors, and a special initiator tRNA. The initiator tRNA interacts with the AUG start codon, and links to a special form of the amino acid methionine that is typically removed from the polypeptide after translation is complete.

In prokaryotes and eukaryotes, the basics of polypeptide elongation are the same, so we will review elongation from the perspective of *E. coli*. The large ribosomal subunit of *E. coli* consists of three compartments: the A site binds incoming

charged tRNAs (tRNAs with their attached specific amino acids). The P site binds charged tRNAs carrying amino acids that have formed bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E site releases dissociated tRNAs so they can be recharged with free amino acids. The ribosome shifts one codon at a time, catalyzing each process that occurs in the three sites. With each step, a charged tRNA enters the complex, the polypeptide becomes one amino acid longer, and an uncharged tRNA departs. The energy for each bond between amino acids is derived from GTP, a molecule similar to ATP ([\[link\]](#)). Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200-amino acid polypeptide could be translated in just 10 seconds.



Termination of translation occurs when a stop

codon (UAA, UAG, or UGA) is encountered. When the ribosome encounters the stop codon, the growing polypeptide is released and the ribosome subunits dissociate and leave the mRNA. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

Concept in Action



Transcribe a gene and translate it to protein using complementary pairing and the genetic code at [this site](#).

Section Summary

The central dogma describes the flow of genetic information in the cell from genes to mRNA to

proteins. Genes are used to make mRNA by the process of transcription; mRNA is used to synthesize proteins by the process of translation. The genetic code is the correspondence between the three-nucleotide mRNA codon and an amino acid. The genetic code is “translated” by the tRNA molecules, which associate a specific codon with a specific amino acid. The genetic code is degenerate because 64 triplet codons in mRNA specify only 20 amino acids and three stop codons. This means that more than one codon corresponds to an amino acid. Almost every species on the planet uses the same genetic code.

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit binds to the mRNA template. Translation begins at the initiating AUG on the mRNA. The formation of bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. The ribosome accepts charged tRNAs, and as it steps along the mRNA, it catalyzes bonding between the new amino acid and the end of the growing polypeptide. The entire mRNA is translated in three-nucleotide “steps” of the ribosome. When a stop codon is encountered, a release factor binds and dissociates the components and frees the new protein.

Multiple Choice

The RNA components of ribosomes are synthesized in the _____.

1. cytoplasm
2. nucleus
3. nucleolus
4. endoplasmic reticulum

C

How long would the peptide be that is translated from this mRNA sequence: 5'-AUGGGCUACCGA-3'?

1. 0
2. 2
3. 3
4. 4

D

Free Response

Transcribe and translate the following DNA sequence (nontemplate strand): 5'-ATGGCCGGTTATTAAGCA-3'

The mRNA would be: 5'-AUGGCCGGUUAUUAAGCA-3'. The protein would be: MAGY. Even though there are six codons, the fifth codon corresponds to a stop, so the sixth codon would not be translated.

Glossary

codon

three consecutive nucleotides in mRNA that specify the addition of a specific amino acid or the release of a polypeptide chain during translation

genetic code

the amino acids that correspond to three-nucleotide codons of mRNA

rRNA

ribosomal RNA; molecules of RNA that combine to form part of the ribosome

stop codon

one of the three mRNA codons that specifies termination of translation

start codon

the AUG (or, rarely GUG) on an mRNA from which translation begins; always specifies methionine

tRNA

transfer RNA; an RNA molecule that contains a specific three-nucleotide anticodon sequence to pair with the mRNA codon and also binds to a specific amino acid

Human Genetics

By the end of this section, you will be able to:

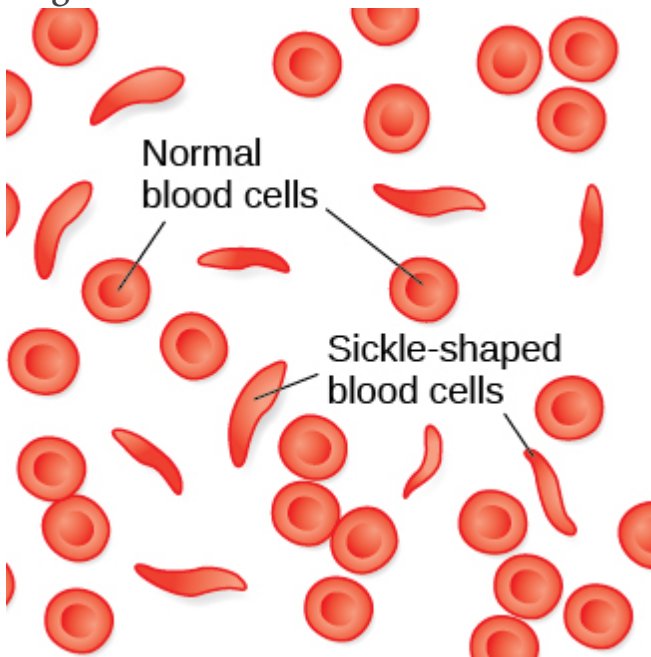
- Explain the basic principles of the theory of evolution by natural selection
- Describe the differences between genotype and phenotype
- Discuss how gene-environment interactions are critical for expression of physical and psychological characteristics

Psychological researchers study genetics in order to better understand the biological basis that contributes to certain behaviors. While all humans share certain biological mechanisms, we are each unique. And while our bodies have many of the same parts—brains and hormones and cells with genetic codes—these are expressed in a wide variety of behaviors, thoughts, and reactions.

Why do two people infected by the same disease have different outcomes: one surviving and one succumbing to the ailment? How are genetic diseases passed through family lines? Are there genetic components to psychological disorders, such as depression or schizophrenia? To what extent might there be a psychological basis to health conditions such as childhood obesity?

To explore these questions, let's start by focusing on a specific disease, sickle-cell anemia, and how it

might affect two infected sisters. Sickle-cell anemia is a genetic condition in which red blood cells, which are normally round, take on a crescent-like shape ([link](#)). The changed shape of these cells affects how they function: sickle-shaped cells can clog blood vessels and block blood flow, leading to high fever, severe pain, swelling, and tissue damage. Normal blood cells travel freely through the blood vessels, while sickle-shaped cells form blockages preventing blood flow.



Many people with sickle-cell anemia—and the particular genetic mutation that causes it—die at an early age. While the notion of “survival of the fittest” may suggest that people suffering from this disease have a low survival rate and therefore the disease will become less common, this is not the

case. Despite the negative evolutionary effects associated with this genetic mutation, the sickle-cell gene remains relatively common among people of African descent. Why is this? The explanation is illustrated with the following scenario.

Imagine two young women—Luwi and Sena—sisters in rural Zambia, Africa. Luwi carries the gene for sickle-cell anemia; Sena does not carry the gene. Sickle-cell carriers have one copy of the sickle-cell gene but do not have full-blown sickle-cell anemia. They experience symptoms only if they are severely dehydrated or are deprived of oxygen (as in mountain climbing). Carriers are thought to be immune from malaria (an often deadly disease that is widespread in tropical climates) because changes in their blood chemistry and immune functioning prevent the malaria parasite from having its effects (Gong, Parikh, Rosenthal, & Greenhouse, 2013). However, full-blown sickle-cell anemia, with two copies of the sickle-cell gene, does not provide immunity to malaria.

While walking home from school, both sisters are bitten by mosquitos carrying the malaria parasite. Luwi does not get malaria because she carries the sickle-cell mutation. Sena, on the other hand, develops malaria and dies just two weeks later. Luwi survives and eventually has children, to whom she may pass on the sickle-cell mutation.



Visit this [website](#) to learn more about how a mutation in DNA leads to sickle-cell anemia.

Malaria is rare in the United States, so the sickle-cell gene benefits nobody: the gene manifests primarily in health problems—minor in carriers, severe in the full-blown disease—with no health benefits for carriers. However, the situation is quite different in other parts of the world. In parts of Africa where malaria is prevalent, having the sickle-cell mutation does provide health benefits for carriers (protection from malaria).

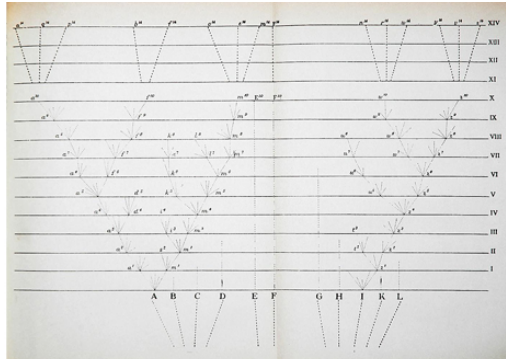
This is precisely the situation that Charles Darwin describes in the **theory of evolution by natural selection** ([\[link\]](#)). In simple terms, the theory states that organisms that are better suited for their environment will survive and reproduce, while those that are poorly suited for their environment will die off. In our example, we can see that as a carrier, Luwi's mutation is highly adaptive in her African homeland; however, if she resided in the

United States (where malaria is much less common), her mutation could prove costly—with a high probability of the disease in her descendants and minor health problems of her own.

(a) In 1859, Charles Darwin proposed his theory of evolution by natural selection in his book, *On the Origin of Species*. (b) The book contains just one illustration: this diagram that shows how species evolve over time through natural selection.



(a)



(b)

Two Perspectives on Genetics and Behavior

It's easy to get confused about two fields that study the interaction of genes and the environment, such as the fields of evolutionary psychology and behavioral genetics. How can we tell them apart? In both fields, it is understood that genes not only code for particular traits, but also contribute to certain patterns of cognition and behavior.

Evolutionary psychology focuses on how universal patterns of behavior and cognitive processes have

evolved over time. Therefore, variations in cognition and behavior would make individuals more or less successful in reproducing and passing those genes to their offspring. Evolutionary psychologists study a variety of psychological phenomena that may have evolved as adaptations, including fear response, food preferences, mate selection, and cooperative behaviors (Confer et al., 2010).

Whereas evolutionary psychologists focus on universal patterns that evolved over millions of years, behavioral geneticists study how individual differences arise, in the present, through the interaction of genes and the environment. When studying human behavior, behavioral geneticists often employ twin and adoption studies to research questions of interest. Twin studies compare the rates that a given behavioral trait is shared among identical and fraternal twins; adoption studies compare those rates among biologically related relatives and adopted relatives. Both approaches provide some insight into the relative importance of genes and environment for the expression of a given trait.



Watch this [interview](#) with renowned evolutionary psychologist David Buss for an explanation of how a psychologist approaches evolution and how this approach fits within the field of social science.

(a) Genotype refers to the genetic makeup of an individual based on the genetic material (DNA) inherited from one's parents. (b) Phenotype describes an individual's observable characteristics, such as hair color, skin color, height, and build. (credit a: modification of work by Caroline Davis; credit b: modification of work by Cory Zanker) (a) A Punnett square is a tool used to predict how genes will interact in the production of offspring. The capital B represents the dominant allele, and the lowercase b represents the recessive allele. In the example of the cleft chin, where B is cleft chin (dominant allele), wherever a pair contains the dominant allele, B, you can expect a cleft chin phenotype. You can expect a smooth chin phenotype only when there are two copies of the recessive allele, bb. (b) A cleft chin, shown here, is an inherited trait. In this Punnett square, N represents the normal allele, and p represents the

recessive allele that is associated with PKU. If two individuals mate who are both heterozygous for the allele associated with PKU, their offspring have a 25% chance of expressing the PKU phenotype.

Genetic Variation

Genetic variation, the genetic difference between individuals, is what contributes to a species' adaptation to its environment. In humans, genetic variation begins with an egg, about 100 million sperm, and fertilization. Fertile women ovulate roughly once per month, releasing an egg from follicles in the ovary. During the egg's journey from the ovary through the fallopian tubes, to the uterus, a sperm may fertilize an egg.

The egg and the sperm each contain 23 chromosomes. **Chromosomes** are long strings of genetic material known as **deoxyribonucleic acid (DNA)**. DNA is a helix-shaped molecule made up of nucleotide base pairs. In each chromosome, sequences of DNA make up **genes** that control or partially control a number of visible characteristics, known as traits, such as eye color, hair color, and so on. A single gene may have multiple possible variations, or alleles. An **allele** is a specific version of a gene. So, a given gene may code for the trait of hair color, and the different alleles of that gene affect which hair color an individual has.

When a sperm and egg fuse, their 23 chromosomes pair up and create a zygote with 23 pairs of chromosomes. Therefore, each parent contributes half the genetic information carried by the offspring; the resulting physical characteristics of the offspring (called the **phenotype**) are determined by the interaction of genetic material supplied by the parents (called the **genotype**). A person's **genotype** is the genetic makeup of that individual.

Phenotype, on the other hand, refers to the individual's inherited physical characteristics, which are a combination of genetic and environmental influences ([\[link\]](#)).



(a)

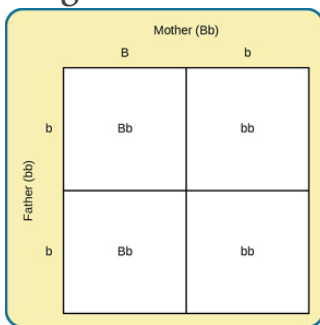


(b)

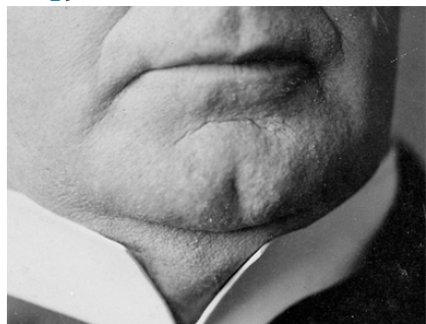
Most traits are controlled by multiple genes, but some traits are controlled by one gene. A characteristic like cleft chin, for example, is influenced by a single gene from each parent. In this example, we will call the gene for cleft chin “B,” and the gene for smooth chin “b.” Cleft chin is a dominant trait, which means that having the **dominant allele** either from one parent (Bb) or both parents (BB) will always result in the phenotype associated with the dominant allele. When someone has two copies of the same allele,

they are said to be **homozygous** for that allele. When someone has a combination of alleles for a given gene, they are said to be **heterozygous**. For example, smooth chin is a recessive trait, which means that an individual will only display the smooth chin phenotype if they are homozygous for that **recessive allele** (bb).

Imagine that a woman with a cleft chin mates with a man with a smooth chin. What type of chin will their child have? The answer to that depends on which alleles each parent carries. If the woman is homozygous for cleft chin (BB), her offspring will always have cleft chin. It gets a little more complicated, however, if the mother is heterozygous for this gene (Bb). Since the father has a smooth chin—therefore homozygous for the recessive allele (bb)—we can expect the offspring to have a 50% chance of having a cleft chin and a 50% chance of having a smooth chin ([\[link\]](#)).



(a)

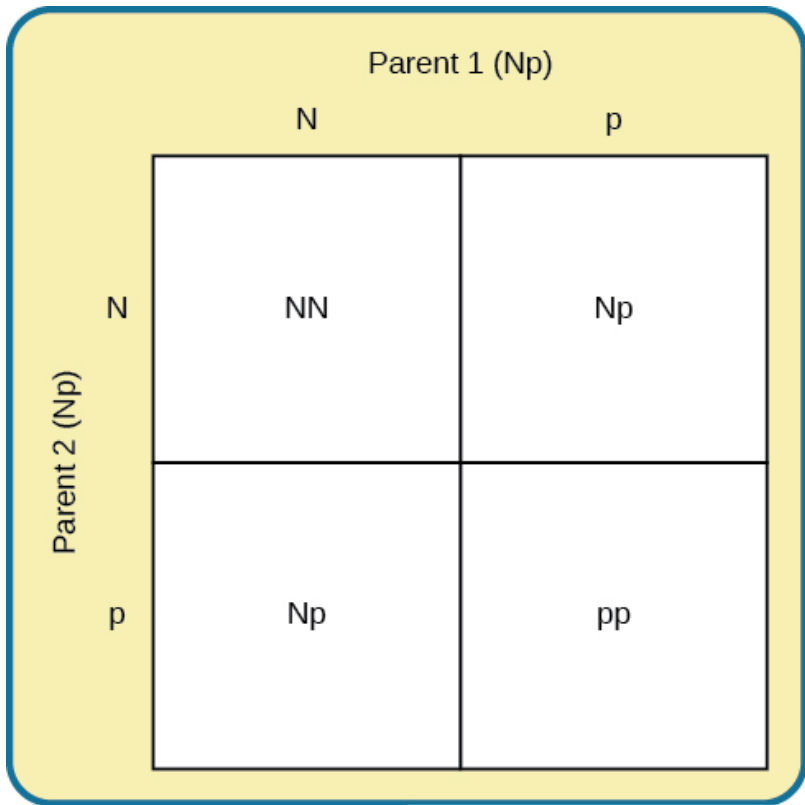


(b)

Sickle-cell anemia is just one of many genetic disorders caused by the pairing of two recessive

genes. For example, phenylketonuria (PKU) is a condition in which individuals lack an enzyme that normally converts harmful amino acids into harmless byproducts. If someone with this condition goes untreated, he or she will experience significant deficits in cognitive function, seizures, and increased risk of various psychiatric disorders. Because PKU is a recessive trait, each parent must have at least one copy of the recessive allele in order to produce a child with the condition ([\[link\]](#)).

So far, we have discussed traits that involve just one gene, but few human characteristics are controlled by a single gene. Most traits are **polygenic**: controlled by more than one gene. Height is one example of a polygenic trait, as are skin color and weight.



Where do harmful genes that contribute to diseases like PKU come from? Gene mutations provide one source of harmful genes. A **mutation** is a sudden, permanent change in a gene. While many mutations can be harmful or lethal, once in a while, a mutation benefits an individual by giving that person an advantage over those who do not have the mutation. Recall that the theory of evolution asserts that individuals best adapted to their particular environments are more likely to reproduce and pass on their genes to future generations. In order for this process to occur, there

must be competition—more technically, there must be variability in genes (and resultant traits) that allow for variation in adaptability to the environment. If a population consisted of identical individuals, then any dramatic changes in the environment would affect everyone in the same way, and there would be no variation in selection. In contrast, diversity in genes and associated traits allows some individuals to perform slightly better than others when faced with environmental change. This creates a distinct advantage for individuals best suited for their environments in terms of successful reproduction and genetic transmission. Nature and nurture work together like complex pieces of a human puzzle. The interaction of our environment and genes makes us the individuals we are. (credit "puzzle": modification of work by Cory Zanker; credit "houses": modification of work by Ben Salter; credit "DNA": modification of work by NHGRI)

Gene-Environment Interactions

Genes do not exist in a vacuum. Although we are all biological organisms, we also exist in an environment that is incredibly important in determining not only when and how our genes express themselves, but also in what combination. Each of us represents a unique interaction between our genetic makeup and our environment; range of reaction is one way to describe this interaction.

Range of reaction asserts that our genes set the boundaries within which we can operate, and our environment interacts with the genes to determine where in that range we will fall. For example, if an individual's genetic makeup predisposes her to high levels of intellectual potential and she is reared in a rich, stimulating environment, then she will be more likely to achieve her full potential than if she were raised under conditions of significant deprivation. According to the concept of range of reaction, genes set definite limits on potential, and environment determines how much of that potential is achieved. Some disagree with this theory and argue that genes do not set a limit on a person's potential.

Another perspective on the interaction between genes and the environment is the concept of **genetic environmental correlation**. Stated simply, our genes influence our environment, and our environment influences the expression of our genes ([link]). Not only do our genes and environment interact, as in range of reaction, but they also influence one another bidirectionally. For example, the child of an NBA player would probably be exposed to basketball from an early age. Such exposure might allow the child to realize his or her full genetic, athletic potential. Thus, the parents' genes, which the child shares, influence the child's environment, and that environment, in turn, is well suited to support the child's genetic potential.



In another approach to gene-environment interactions, the field of **epigenetics** looks beyond the genotype itself and studies how the same genotype can be expressed in different ways. In other words, researchers study how the same genotype can lead to very different phenotypes. As mentioned earlier, gene expression is often influenced by environmental context in ways that are not entirely obvious. For instance, identical twins share the same genetic information (**identical twins** develop from a single fertilized egg that split, so the genetic material is exactly the same in each; in contrast, **fraternal twins** develop from two different eggs fertilized by different sperm, so the genetic material varies as with non-twin siblings). But even with identical genes, there remains an incredible amount of variability in how gene expression can unfold over the course of each twin's

life. Sometimes, one twin will develop a disease and the other will not. In one example, Tiffany, an identical twin, died from cancer at age 7, but her twin, now 19 years old, has never had cancer. Although these individuals share an identical genotype, their phenotypes differ as a result of how that genetic information is expressed over time. The epigenetic perspective is very different from range of reaction, because here the genotype is not fixed and limited.



Visit this [site](#) for an engaging video primer on the epigenetics of twin studies.

Genes affect more than our physical characteristics. Indeed, scientists have found genetic linkages to a number of behavioral characteristics, ranging from basic personality traits to sexual orientation to spirituality (for examples, see Mustanski et al., 2005; Comings, Gonzales, Saucier, Johnson, &

MacMurray, 2000). Genes are also associated with temperament and a number of psychological disorders, such as depression and schizophrenia. So while it is true that genes provide the biological blueprints for our cells, tissues, organs, and body, they also have significant impact on our experiences and our behaviors.

Let's look at the following findings regarding schizophrenia in light of our three views of gene-environment interactions. Which view do you think best explains this evidence?

In a study of people who were given up for adoption, adoptees whose biological mothers had schizophrenia *and* who had been raised in a disturbed family environment were much more likely to develop schizophrenia or another psychotic disorder than were any of the other groups in the study:

- Of adoptees whose biological mothers had schizophrenia (high genetic risk) and who were raised in disturbed family environments, 36.8% were likely to develop schizophrenia.
- Of adoptees whose biological mothers had schizophrenia (high genetic risk) and who were raised in healthy family environments, 5.8% were likely to develop schizophrenia.
- Of adoptees with a low genetic risk (whose mothers did not have schizophrenia) and who

- were raised in disturbed family environments, 5.3% were likely to develop schizophrenia.
- Of adoptees with a low genetic risk (whose mothers did not have schizophrenia) and who were raised in healthy family environments, 4.8% were likely to develop schizophrenia (Tienari et al., 2004).

The study shows that adoptees with high genetic risk were especially likely to develop schizophrenia only if they were raised in disturbed home environments. This research lends credibility to the notion that both genetic vulnerability and environmental stress are necessary for schizophrenia to develop, and that genes alone do not tell the full tale.

Summary

Genes are sequences of DNA that code for a particular trait. Different versions of a gene are called alleles—sometimes alleles can be classified as dominant or recessive. A dominant allele always results in the dominant phenotype. In order to exhibit a recessive phenotype, an individual must be homozygous for the recessive allele. Genes affect both physical and psychological characteristics. Ultimately, how and when a gene is expressed, and what the outcome will be—in terms of both physical and psychological characteristics—is a function of

the interaction between our genes and our environments.

Review Questions

A(n) _____ is a sudden, permanent change in a sequence of DNA.

- A. allele
- B. chromosome
- C. epigenetic
- D. mutation

D

_____ refers to a person's genetic makeup, while _____ refers to a person's physical characteristics.

- A. Phenotype; genotype
- B. Genotype; phenotype
- C. DNA; gene
- D. Gene; DNA

B

_____ is the field of study that focuses on genes and their expression.

- A. Social psychology
- B. Evolutionary psychology
- C. Epigenetics
- D. Behavioral neuroscience

C

Humans have _____ pairs of chromosomes.

- A. 15
- B. 23
- C. 46
- D. 78

B

Critical Thinking Questions

The theory of evolution by natural selection requires variability of a given trait. Why is variability necessary and where does it come from?

Variability is essential for natural selection to work. If all individuals are the same on a given trait, there will be no relative difference in their reproductive success because everyone will be equally adapted to their environments on that trait. Mutations are one source of variability, but sexual reproduction is another important source of variation given that individuals inherit half of their genetic makeup from each of their parents.

Personal Application Questions

You share half of your genetic makeup with each of your parents, but you are no doubt very different from both of them. Spend a few minutes jotting down the similarities and differences between you and your parents. How do you think your unique environment and experiences have contributed to some of the differences you see?

Glossary

allele

specific version of a gene

chromosome

long strand of genetic information

deoxyribonucleic acid (DNA)

helix-shaped molecule made of nucleotide base pairs

dominant allele

allele whose phenotype will be expressed in an individual that possesses that allele

epigenetics

study of gene-environment interactions, such as how the same genotype leads to different phenotypes

fraternal twins

twins who develop from two different eggs fertilized by different sperm, so their genetic material varies the same as in non-twin siblings

gene

sequence of DNA that controls or partially controls physical characteristics

genetic environmental correlation

view of gene-environment interaction that asserts our genes affect our environment, and our environment influences the expression of our genes

genotype

genetic makeup of an individual

heterozygous

consisting of two different alleles

homozygous

consisting of two identical alleles

identical twins

twins that develop from the same sperm and egg

mutation

sudden, permanent change in a gene

phenotype

individual's inheritable physical characteristics

polygenic

multiple genes affecting a given trait

range of reaction

asserts our genes set the boundaries within which we can operate, and our environment interacts with the genes to determine where in that range we will fall

recessive allele

allele whose phenotype will be expressed only if an individual is homozygous for that allele

theory of evolution by natural selection

states that organisms that are better suited for their environments will survive and reproduce compared to those that are poorly suited for their environments

Laws of Inheritance

By the end of this section, you will be able to:

- Explain the relationship between genotypes and phenotypes in dominant and recessive gene systems
- Use a Punnett square to calculate the expected proportions of genotypes and phenotypes in a monohybrid cross
- Explain Mendel's law of segregation and independent assortment in terms of genetics and the events of meiosis
- Explain the purpose and methods of a test cross

The seven characteristics that Mendel evaluated in his pea plants were each expressed as one of two versions, or traits. Mendel deduced from his results that each individual had two discrete copies of the characteristic that are passed individually to offspring. We now call those two copies genes, which are carried on chromosomes. The reason we have two copies of each gene is that we inherit one from each parent. In fact, it is the chromosomes we inherit and the two copies of each gene are located on paired chromosomes. Recall that in meiosis these chromosomes are separated out into haploid gametes. This separation, or segregation, of the homologous chromosomes means also that only one of the copies of the gene gets moved into a gamete. The offspring are formed when that gamete unites with one from another parent and the two copies of

each gene (and chromosome) are restored.

For cases in which a single gene controls a single characteristic, a diploid organism has two genetic copies that may or may not encode the same version of that characteristic. For example, one individual may carry a gene that determines white flower color and a gene that determines violet flower color. Gene variants that arise by mutation and exist at the same relative locations on homologous chromosomes are called **alleles**. Mendel examined the inheritance of genes with just two allele forms, but it is common to encounter more than two alleles for any given gene in a natural population.

Phenotypes are physical expressions of traits that are transmitted by alleles. Capital letters represent dominant alleles and lowercase letters represent recessive alleles. The phenotypic ratios are the ratios of visible characteristics. The genotypic ratios are the ratios of gene combinations in the offspring, and these are not always distinguishable in the phenotypes. The allele for albinism, expressed here in humans, is recessive. Both of this child's parents carried the recessive allele.

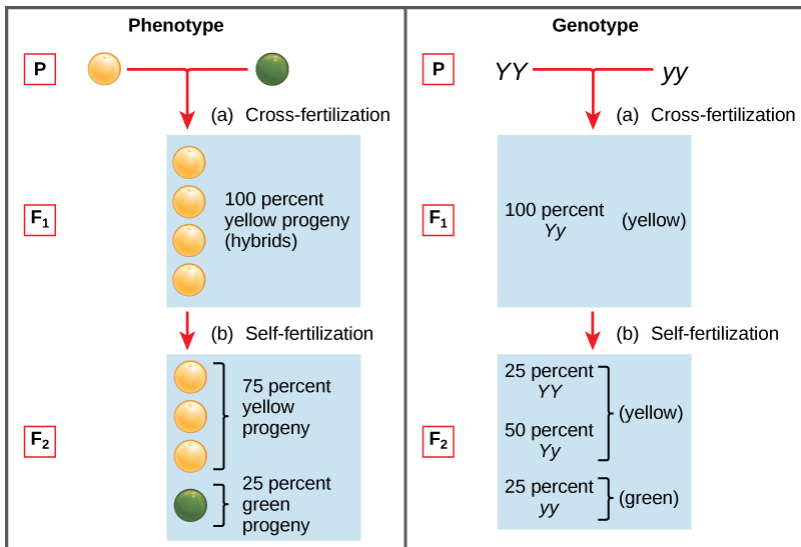
Phenotypes and Genotypes

Two alleles for a given gene in a diploid organism are expressed and interact to produce physical characteristics. The observable traits expressed by an organism are referred to as its **phenotype**. An

organism's underlying genetic makeup, consisting of both the physically visible and the non-expressed alleles, is called its **genotype**. Mendel's hybridization experiments demonstrate the difference between phenotype and genotype. For example, the phenotypes that Mendel observed in his crosses between pea plants with differing traits are connected to the diploid genotypes of the plants in the P, F₁, and F₂ generations. We will use a second trait that Mendel investigated, seed color, as an example. Seed color is governed by a single gene with two alleles. The yellow-seed allele is dominant and the green-seed allele is recessive. When true-breeding plants were cross-fertilized, in which one parent had yellow seeds and one had green seeds, all of the F₁ hybrid offspring had yellow seeds. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with yellow seeds. However, we know that the allele donated by the parent with green seeds was not simply lost because it reappeared in some of the F₂ offspring ([\[link\]](#)). Therefore, the F₁ plants must have been genotypically different from the parent with yellow seeds.

The P plants that Mendel used in his experiments were each homozygous for the trait he was studying. Diploid organisms that are **homozygous** for a gene have two identical alleles, one on each of their homologous chromosomes. The genotype is often written as YY or yy, for which each letter

represents one of the two alleles in the genotype. The dominant allele is capitalized and the recessive allele is lower case. The letter used for the gene (seed color in this case) is usually related to the dominant trait (yellow allele, in this case, or “Y”). Mendel’s parental pea plants always bred true because both produced gametes carried the same allele. When P plants with contrasting traits were cross-fertilized, all of the offspring were **heterozygous** for the contrasting trait, meaning their genotype had different alleles for the gene being examined. For example, the F₁ yellow plants that received a Y allele from their yellow parent and a y allele from their green parent had the genotype Yy.



Law of Dominance

Our discussion of homozygous and heterozygous

organisms brings us to why the F1 heterozygous offspring were identical to one of the parents, rather than expressing both alleles. In all seven pea-plant characteristics, one of the two contrasting alleles was dominant, and the other was recessive. Mendel called the dominant allele the expressed unit factor; the recessive allele was referred to as the latent unit factor. We now know that these so-called unit factors are actually genes on homologous chromosomes. For a gene that is expressed in a dominant and recessive pattern, homozygous dominant and heterozygous organisms will look identical (that is, they will have different genotypes but the same phenotype), and the recessive allele will only be observed in homozygous recessive individuals ([\[link\]](#)).

**Correspondence
between
Genotype
and
Phenotype
for a
Dominant-
Recessive
Characteristic.**

	Homozygous dominant	Heterozygous	Homozygous recessive
Genotype	AA	Aa	aa
Phenotype	Dominant	Dominant	Recessive

Genotype	YY	Yy	yy
Phenotype	yellow	yellow	green

Mendel's **law of dominance** states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. For example, when crossing true-breeding violet-flowered plants with true-breeding white-flowered plants, all of the offspring were violet-flowered, even though they all had one allele for violet and one allele for white. Rather than both alleles contributing to a phenotype, the dominant allele will be expressed exclusively. The recessive allele will remain latent, but will be transmitted to offspring in the same manner as that by which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele ([link](#)), and these offspring will breed true when self-crossed.



Monohybrid Cross and the Punnett Square

When fertilization occurs between two true-breeding parents that differ by only the characteristic being studied, the process is called a **monohybrid** cross, and the resulting offspring are called monohybrids. Mendel performed seven types of monohybrid

crosses, each involving contrasting traits for different characteristics. Out of these crosses, all of the F₁ offspring had the phenotype of one parent, and the F₂ offspring had a 3:1 phenotypic ratio. On the basis of these results, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring, and every possible combination of unit factors was equally likely.

The results of Mendel's research can be explained in terms of probabilities, which are mathematical measures of likelihood. The probability of an event is calculated by the number of times the event occurs divided by the total number of opportunities for the event to occur. A probability of one (100 percent) for some event indicates that it is guaranteed to occur, whereas a probability of zero (0 percent) indicates that it is guaranteed to not occur, and a probability of 0.5 (50 percent) means it has an equal chance of occurring or not occurring.

To demonstrate this with a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green seeds. The dominant seed color is yellow; therefore, the parental genotypes were YY for the plants with yellow seeds and yy for the plants with green seeds. A **Punnett square**, devised by the British geneticist Reginald Punnett, is useful for determining probabilities because it is drawn to predict all possible outcomes of all possible random

fertilization events and their expected frequencies. [\[link\]](#) shows a Punnett square for a cross between a plant with yellow peas and one with green peas. To prepare a Punnett square, all possible combinations of the parental alleles (the genotypes of the gametes) are listed along the top (for one parent) and side (for the other parent) of a grid. The combinations of egg and sperm gametes are then made in the boxes in the table on the basis of which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant and recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible in the F₁ offspring. All offspring are Yy and have yellow seeds.

When the F₁ offspring are crossed with each other, each has an equal probability of contributing either a Y or a y to the F₂ offspring. The result is a 1 in 4 (25 percent) probability of both parents contributing a Y, resulting in an offspring with a yellow phenotype; a 25 percent probability of parent A contributing a Y and parent B a y, resulting in offspring with a yellow phenotype; a 25 percent probability of parent A contributing a y and parent B a Y, also resulting in a yellow phenotype; and a

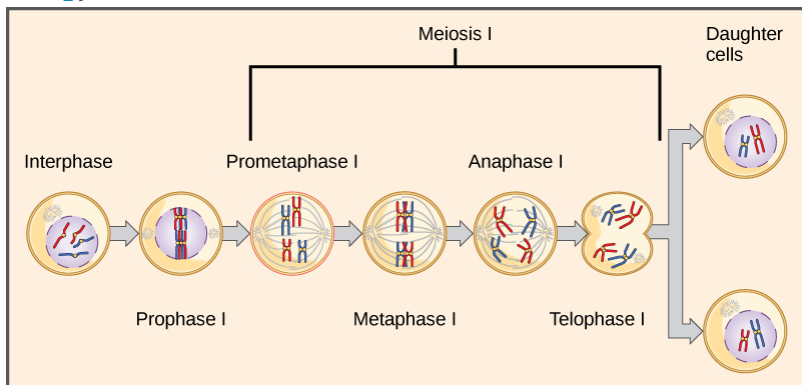
(25 percent) probability of both parents contributing a y , resulting in a green phenotype. When counting all four possible outcomes, there is a 3 in 4 probability of offspring having the yellow phenotype and a 1 in 4 probability of offspring having the green phenotype. This explains why the results of Mendel's F₂ generation occurred in a 3:1 phenotypic ratio. Using large numbers of crosses, Mendel was able to calculate probabilities, found that they fit the model of inheritance, and use these to predict the outcomes of other crosses.

The first division in meiosis is shown. A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

Law of Segregation

Observing that true-breeding pea plants with contrasting traits gave rise to F₁ generations that all expressed the dominant trait and F₂ generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the **law of segregation**. This law states that paired unit factors (genes) must segregate equally into gametes such that offspring have an equal likelihood of inheriting either factor. For the F₂ generation of a monohybrid cross, the following three possible combinations of genotypes result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one

dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes. The physical basis of Mendel's law of segregation is the first division of meiosis in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. This process was not understood by the scientific community during Mendel's lifetime ([link]).



Test Cross

Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the **test**

cross, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F₁ offspring will be heterozygotes expressing the dominant trait ([\[link\]](#)). Alternatively, if the dominant-expressing organism is a heterozygote, the F₁ offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes ([\[link\]](#)). The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.



The Test Cross

Gametes from parent
of unknown genotype

Y

?

Gametes from
recessive parent
y
y

A test cross resulting in
all dominant offspring
indicates that the parent
is homozygous dominant.

Gametes from parent
of unknown genotype

Y

?

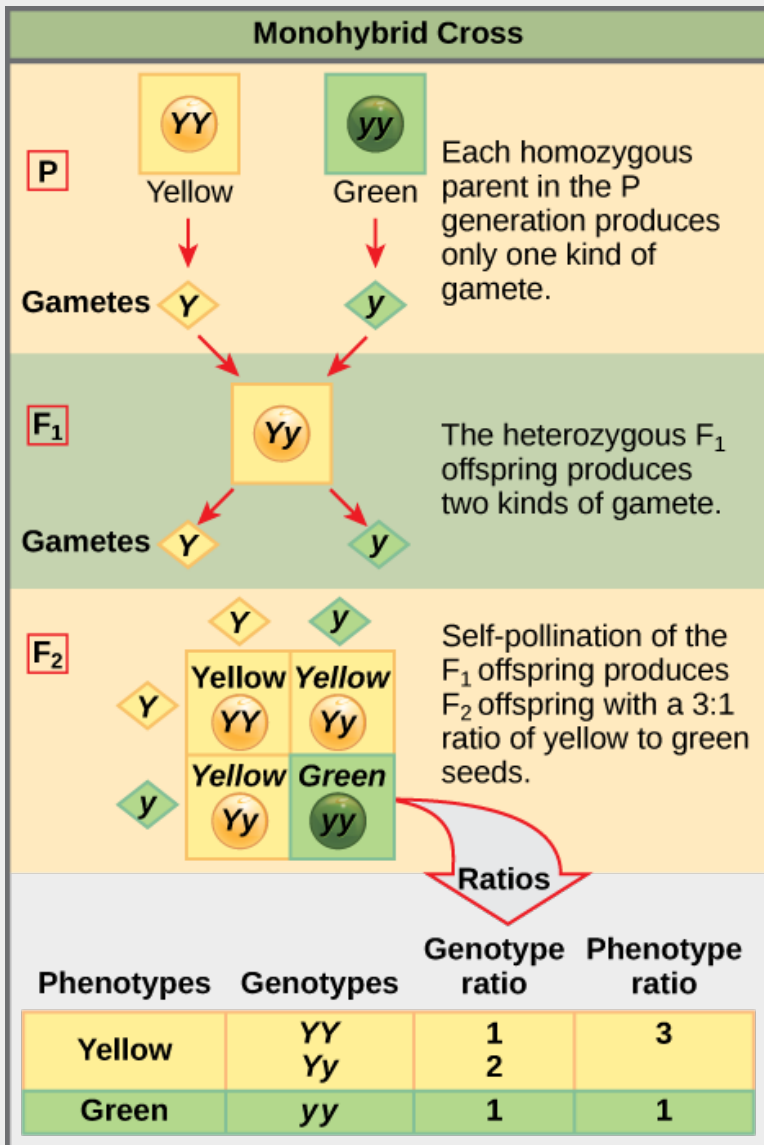
Gametes from
recessive parent
y
y

A test cross resulting
in a 1:1 ratio of yellow
to green offspring
indicates that the
parent is heterozygous.

Art Connection

This Punnett square shows the cross between plants with yellow seeds and green seeds. The cross between the true-breeding P plants produces F₁ heterozygotes that can be self-fertilized. The self-cross of the F₁ generation can be analyzed with a

Punnett square to predict the genotypes of the F₂ generation. Given an inheritance pattern of dominant–recessive, the genotypic and phenotypic ratios can then be determined.



In pea plants, round peas (*R*) are dominant to wrinkled peas (*r*). You do a test cross between a

pea plant with wrinkled peas (genotype rr) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

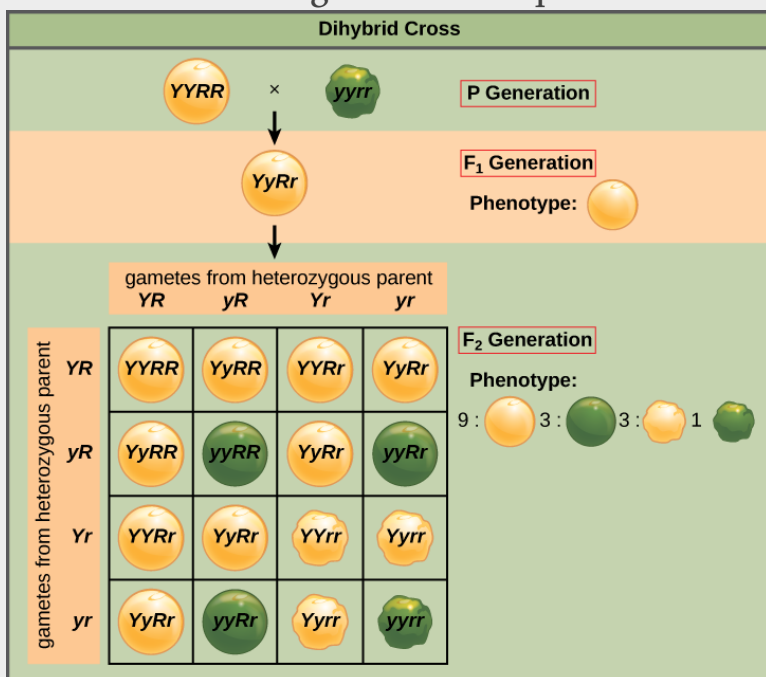
The random segregation into daughter nuclei that happens during the first division in meiosis can lead to a variety of possible genetic arrangements.

Law of Independent Assortment

Mendel's **law of independent assortment** states that genes do not influence each other with regard to the sorting of alleles into gametes, and every possible combination of alleles for every gene is equally likely to occur. Independent assortment of genes can be illustrated by the **dihybrid** cross, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants, one that has wrinkled, green seeds ($rryy$) and another that has round, yellow seeds ($RRYY$). Because each parent is homozygous, the law of segregation indicates that the gametes for the wrinkled–green plant all are ry , and the gametes for the round–yellow plant are all RY . Therefore, the F_1 generation of offspring all are $RrYy$ ([\[link\]](#)).

Art Connection

A dihybrid cross in pea plants involves the genes for seed color and texture. The P cross produces F₁ offspring that are all heterozygous for both characteristics. The resulting 9:3:3:1 F₂ phenotypic ratio is obtained using a Punnett square.

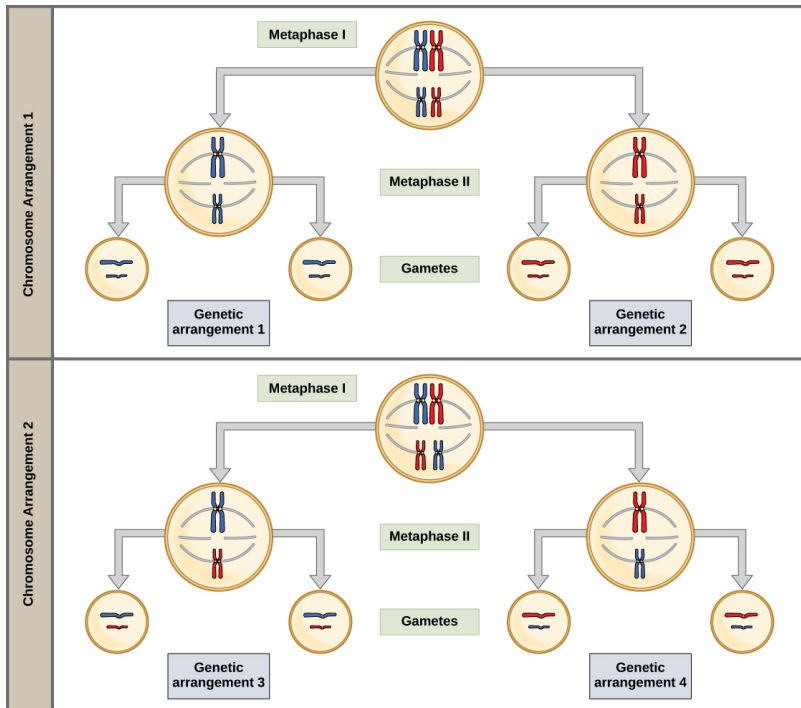


In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

The gametes produced by the F₁ individuals must

have one allele from each of the two genes. For example, a gamete could get an R allele for the seed shape gene and either a Y or a y allele for the seed color gene. It cannot get both an R and an r allele; each gamete can have only one allele per gene. The law of independent assortment states that a gamete into which an r allele is sorted would be equally likely to contain either a Y or a y allele. Thus, there are four equally likely gametes that can be formed when the $RrYy$ heterozygote is self-crossed, as follows: RY , rY , Ry , and ry . Arranging these gametes along the top and left of a 4×4 Punnett square ([\[link\]](#)) gives us 16 equally likely genotypic combinations. From these genotypes, we find a phenotypic ratio of 9 round–yellow:3 round–green:3 wrinkled–yellow:1 wrinkled–green ([\[link\]](#)). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

The physical basis for the law of independent assortment also lies in meiosis I, in which the different homologous pairs line up in random orientations. Each gamete can contain any combination of paternal and maternal chromosomes (and therefore the genes on them) because the orientation of tetrads on the metaphase plane is random ([\[link\]](#)).



Section Summary

When true-breeding, or homozygous, individuals that differ for a certain trait are crossed, all of the offspring will be heterozygous for that trait. If the traits are inherited as dominant and recessive, the F₁ offspring will all exhibit the same phenotype as the parent homozygous for the dominant trait. If these heterozygous offspring are self-crossed, the resulting F₂ offspring will be equally likely to inherit gametes carrying the dominant or recessive trait, giving rise to offspring of which one quarter are homozygous dominant, half are heterozygous, and

one quarter are homozygous recessive. Because homozygous dominant and heterozygous individuals are phenotypically identical, the observed traits in the F₂ offspring will exhibit a ratio of three dominant to one recessive.

Mendel postulated that genes (characteristics) are inherited as pairs of alleles (traits) that behave in a dominant and recessive pattern. Alleles segregate into gametes such that each gamete is equally likely to receive either one of the two alleles present in a diploid individual. In addition, genes are assorted into gametes independently of one another. That is, in general, alleles are not more likely to segregate into a gamete with a particular allele of another gene.

Art Connections

[\[link\]](#) In pea plants, round peas (R) are dominant to wrinkled peas (r). You do a test cross between a pea plant with wrinkled peas (genotype rr) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

[\[link\]](#) You cannot be sure if the plant is homozygous or heterozygous as the data set is too small: by random chance, all three plants might have acquired only the dominant gene even if the recessive one is present.

[\[link\]](#) In pea plants, purple flowers (P) are dominant to white (p), and yellow peas (Y) are dominant to green (y). What are the possible genotypes and phenotypes for a cross between $PpYY$ and $ppYy$ pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

[\[link\]](#) The possible genotypes are $PpYY$, $PpYy$, $ppYY$, and $ppYy$. The former two genotypes would result in plants with purple flowers and yellow peas, while the latter two genotypes would result in plants with white flowers with yellow peas, for a 1:1 ratio of each phenotype. You only need a 2×2 Punnett square (four squares total) to do this analysis because two of the alleles are homozygous.

Multiple Choice

The observable traits expressed by an organism are described as its _____.

1. phenotype
2. genotype
3. alleles
4. zygote

A

A recessive trait will be observed in individuals that are _____ for that trait.

1. heterozygous
2. homozygous or heterozygous
3. homozygous
4. diploid

C

What are the types of gametes that can be produced by an individual with the genotype *AaBb*?

1. *Aa, Bb*
2. *AA, aa, BB, bb*
3. *AB, Ab, aB, ab*
4. *AB, ab*

C

What is the reason for doing a test cross?

1. to identify heterozygous individuals with the dominant phenotype
2. to determine which allele is dominant and which is recessive
3. to identify homozygous recessive individuals in the F₂
4. to determine if two genes assort independently

A

Free Response

Use a Punnett square to predict the offspring in a cross between a dwarf pea plant (homozygous recessive) and a tall pea plant (heterozygous). What is the phenotypic ratio of the offspring?

The Punnett square would be 2×2 and will have T and T along the top and T and t along the left side. Clockwise from the top left, the

genotypes listed within the boxes will be Tt , Tt , tt , and tt . The phenotypic ratio will be 1 tall:1 dwarf.

Use a Punnett square to predict the offspring in a cross between a tall pea plant (heterozygous) and a tall pea plant (heterozygous). What is the genotypic ratio of the offspring?

The Punnett square will be 2×2 and will have T and t along the top and T and t along the left side. Clockwise from the top left, the genotypes listed within the boxes will be TT , Tt , Tt , and tt . The genotypic ratio will be $1TT:2Tt:1tt$.

Glossary

allele

one of two or more variants of a gene that determines a particular trait for a characteristic

dihybrid

the result of a cross between two true-breeding parents that express different traits for two characteristics

genotype

the underlying genetic makeup, consisting of

both physically visible and non-expressed alleles, of an organism

heterozygous

having two different alleles for a given gene on the homologous chromosomes

homozygous

having two identical alleles for a given gene on the homologous chromosomes

law of dominance

in a heterozygote, one trait will conceal the presence of another trait for the same characteristic

law of independent assortment

genes do not influence each other with regard to sorting of alleles into gametes; every possible combination of alleles is equally likely to occur

law of segregation

paired unit factors (i.e., genes) segregate equally into gametes such that offspring have an equal likelihood of inheriting any combination of factors

monohybrid

the result of a cross between two true-breeding parents that express different traits for only one characteristic

phenotype

the observable traits expressed by an organism

Punnett square

a visual representation of a cross between two individuals in which the gametes of each individual are denoted along the top and side of a grid, respectively, and the possible zygotic genotypes are recombined at each box in the grid

test cross

a cross between a dominant expressing individual with an unknown genotype and a homozygous recessive individual; the offspring phenotypes indicate whether the unknown parent is heterozygous or homozygous for the dominant trait

Extensions of the Laws of Inheritance

By the end of this section, you will be able to:

- Identify non-Mendelian inheritance patterns such as incomplete dominance, codominance, multiple alleles, and sex linkage from the results of crosses
- Explain the effect of linkage and recombination on gamete genotypes
- Explain the phenotypic outcomes of epistatic effects among genes

Mendel studied traits with only one mode of inheritance in pea plants. The inheritance of the traits he studied all followed the relatively simple pattern of dominant and recessive alleles for a single characteristic. There are several important modes of inheritance, discovered after Mendel's work, that do not follow the dominant and recessive, single-gene model.

These pink flowers of a heterozygote snapdragon result from incomplete dominance. (credit: "storebukkebruse"/Flickr) This Punnet square shows an AB/AB blood type cross Inheritance of the ABO blood system in humans is shown. In *Drosophila*, the gene for eye color is located on the X chromosome. Red eye color is wild-type and is dominant to white eye color.

Alternatives to Dominance and

Recessiveness

Mendel's experiments with pea plants suggested that: 1) two types of "units" or alleles exist for every gene; 2) alleles maintain their integrity in each generation (no blending); and 3) in the presence of the dominant allele, the recessive allele is hidden, with no contribution to the phenotype. Therefore, recessive alleles can be "carried" and not expressed by individuals. Such heterozygous individuals are sometimes referred to as "carriers." Since then, genetic studies in other organisms have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true. In the sections to follow, we consider some of the extensions of Mendelism.

Incomplete Dominance

Mendel's results, demonstrating that traits are inherited as dominant and recessive pairs, contradicted the view at that time that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be intermediate between the two parents. For example, in the snapdragon, *Antirrhinum majus* ([\[link\]](#)), a cross between a homozygous parent with white flowers ($CWCW$) and a homozygous parent with red flowers ($CRCR$) will produce offspring with pink flowers ($CRCW$). (Note that different genotypic abbreviations are used for Mendelian extensions to

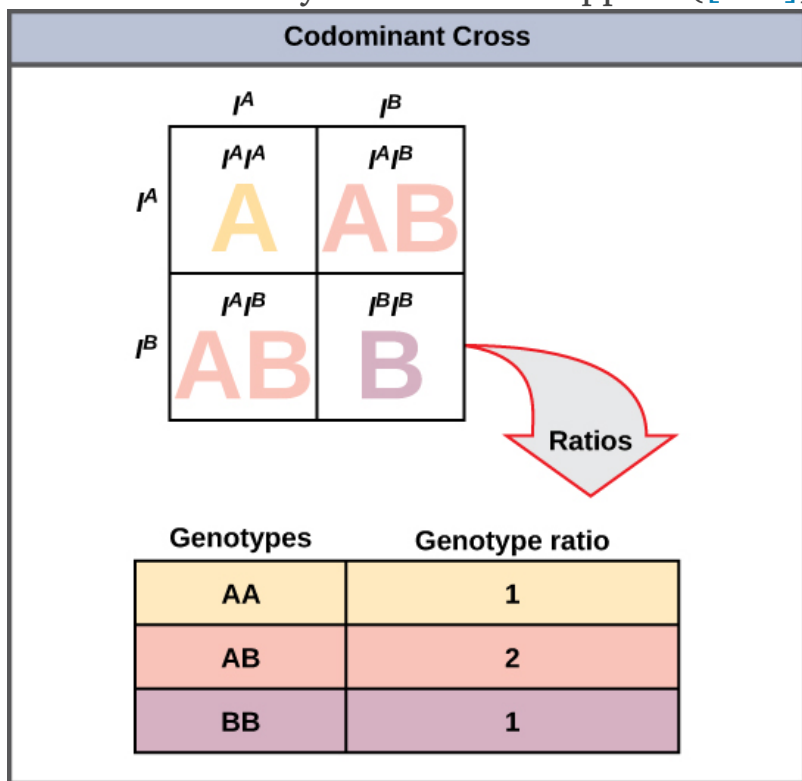
distinguish these patterns from simple dominance and recessiveness.) This pattern of inheritance is described as **incomplete dominance**, meaning that one of the alleles appears in the phenotype in the heterozygote, but not to the exclusion of the other, which can also be seen. The allele for red flowers is incompletely dominant over the allele for white flowers. However, the results of a heterozygote self-cross can still be predicted, just as with Mendelian dominant and recessive crosses. In this case, the genotypic ratio would be 1 $CRCR$:2 $CRCW$:1 $CWCW$, and the phenotypic ratio would be 1:2:1 for red:pink:white. The basis for the intermediate color in the heterozygote is simply that the pigment produced by the red allele (anthocyanin) is diluted in the heterozygote and therefore appears pink because of the white background of the flower petals.



Codominance

A variation on incomplete dominance is **codominance**, in which both alleles for the same characteristic are simultaneously expressed in the heterozygote. An example of codominance occurs in the ABO blood groups of humans. The A and B alleles are expressed in the form of A or B molecules

present on the surface of red blood cells. Homozygotes ($I^A I^A$ and $I^B I^B$) express either the A or the B phenotype, and heterozygotes ($I^A I^B$) express both phenotypes equally. The $I^A I^B$ individual has blood type AB. In a self-cross between heterozygotes expressing a codominant trait, the three possible offspring genotypes are phenotypically distinct. However, the 1:2:1 genotypic ratio characteristic of a Mendelian monohybrid cross still applies ([\[link\]](#)).



Multiple Alleles

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We

now know that this is an oversimplification. Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple alleles may exist at the population level, such that many combinations of two alleles are observed. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype in the natural population as the **wild type** (often abbreviated “+”). All other phenotypes or genotypes are considered variants (mutants) of this typical form, meaning they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is the ABO blood-type system in humans. In this case, there are three alleles circulating in the population. The I_A allele codes for A molecules on the red blood cells, the I_B allele codes for B molecules on the surface of red blood cells, and the i allele codes for no molecules on the red blood cells. In this case, the I_A and I_B alleles are codominant with each other and are both dominant over the i allele. Although there are three alleles present in a population, each individual only gets two of the alleles from their parents. This produces the genotypes and phenotypes shown in [\[link\]](#). Notice that instead of three genotypes, there are six different genotypes when there are three alleles. The number of possible phenotypes depends on the dominance relationships between the three

alleles.

Inheritance of the ABO Blood System in Humans			
	I^A	I^B	i
I^A	$I^A I^A$ A	$I^A I^B$ AB	$I^A i$ A
I^B	$I^B I^A$ AB	$I^B I^B$ B	$I^B i$ B
i	$i I^A$ A	$i I^B$ B	$i i$ O

Evolution in Action

Multiple Alleles Confer Drug Resistance in the Malaria Parasite

Malaria is a parasitic disease in humans that is transmitted by infected female mosquitoes, including *Anopheles gambiae*, and is characterized by cyclic high fevers, chills, flu-like symptoms, and severe anemia. *Plasmodium falciparum* and *P. vivax* are the most common causative agents of malaria, and *P. falciparum* is the most deadly. When promptly and correctly treated, *P. falciparum* malaria has a mortality rate of 0.1 percent. However, in some parts of the world, the parasite has evolved resistance to commonly used malaria

treatments, so the most effective malarial treatments can vary by geographic region. In Southeast Asia, Africa, and South America, *P. falciparum* has developed resistance to the anti-malarial drugs chloroquine, mefloquine, and sulfadoxine-pyrimethamine. *P. falciparum*, which is haploid during the life stage in which it is infective to humans, has evolved multiple drug-resistant mutant alleles of the *dhps* gene. Varying degrees of sulfadoxine resistance are associated with each of these alleles. Being haploid, *P. falciparum* needs only one drug-resistant allele to express this trait. In Southeast Asia, different sulfadoxine-resistant alleles of the *dhps* gene are localized to different geographic regions. This is a common evolutionary phenomenon that comes about because drug-resistant mutants arise in a population and interbreed with other *P. falciparum* isolates in close proximity. Sulfadoxine-resistant parasites cause considerable human hardship in regions in which this drug is widely used as an over-the-counter malaria remedy. As is common with pathogens that multiply to large numbers within an infection cycle, *P. falciparum* evolves relatively rapidly (over a decade or so) in response to the selective pressure of commonly used anti-malarial drugs. For this reason, scientists must constantly work to develop new drugs or drug combinations to combat the worldwide malaria burden. [\[footnote\]](#)

Sumiti Vinayak et al., "Origin and Evolution of Sulfadoxine Resistant *Plasmodium falciparum*," *PLoS*

Sex-Linked Traits

In humans, as well as in many other animals and some plants, the sex of the individual is determined by sex chromosomes—one pair of non-homologous chromosomes. Until now, we have only considered inheritance patterns among non-sex chromosomes, or autosomes. In addition to 22 homologous pairs of autosomes, human females have a homologous pair of X chromosomes, whereas human males have an XY chromosome pair. Although the Y chromosome contains a small region of similarity to the X chromosome so that they can pair during meiosis, the Y chromosome is much shorter and contains fewer genes. When a gene being examined is present on the X, but not the Y, chromosome, it is **X-linked**.

Eye color in *Drosophila*, the common fruit fly, was the first X-linked trait to be identified. Thomas Hunt Morgan mapped this trait to the X chromosome in 1910. Like humans, *Drosophila* males have an XY chromosome pair, and females are XX. In flies the wild-type eye color is red (X_w) and is dominant to white eye color (X_w) ([\[link\]](#)). Because of the location of the eye-color gene, reciprocal crosses do not produce the same offspring ratios. Males are said to be **hemizygous**, in that they have only one

allele for any X-linked characteristic. Hemizyosity makes descriptions of dominance and recessiveness irrelevant for XY males. *Drosophila* males lack the white gene on the Y chromosome; that is, their genotype can only be X^wY or X^WY . In contrast, females have two allele copies of this gene and can be X^wX^w , X^WX^w , or X^wX^W .

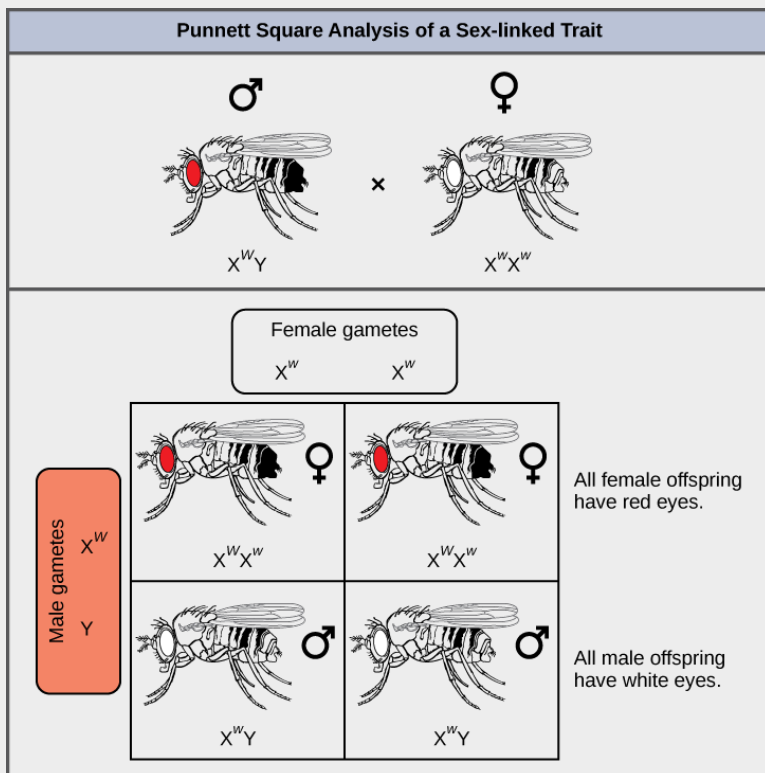


In an X-linked cross, the genotypes of F₁ and F₂ offspring depend on whether the recessive trait was expressed by the male or the female in the P generation. With respect to *Drosophila* eye color, when the P male expresses the white-eye phenotype and the female is homozygously red-eyed, all members of the F₁ generation exhibit red eyes ([\[link\]](#)). The F₁ females are heterozygous (X^WX^w), and the males are all X^wY , having received their X

chromosome from the homozygous dominant P female and their Y chromosome from the P male. A subsequent cross between the $X^W X^w$ female and the $X^w Y$ male would produce only red-eyed females (with $X^W X^W$ or $X^W X^w$ genotypes) and both red- and white-eyed males (with $X^w Y$ or $X^W Y$ genotypes). Now, consider a cross between a homozygous white-eyed female and a male with red eyes. The F₁ generation would exhibit only heterozygous red-eyed females ($X^W X^w$) and only white-eyed males ($X^w Y$). Half of the F₂ females would be red-eyed ($X^W X^W$) and half would be white-eyed ($X^w X^w$). Similarly, half of the F₂ males would be red-eyed ($X^W Y$) and half would be white-eyed ($X^w Y$).

Art Connection

Crosses involving sex-linked traits often give rise to different phenotypes for the different sexes of offspring, as is the case for this cross involving red and white eye color in *Drosophila*. In the diagram, w is the white-eye mutant allele and W is the wild-type, red-eye allele.



What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Discoveries in fruit fly genetics can be applied to human genetics. When a female parent is homozygous for a recessive X-linked trait, she will pass the trait on to 100 percent of her male offspring, because the males will receive the Y chromosome from the male parent. In humans, the alleles for certain conditions (some color-blindness, hemophilia, and muscular dystrophy) are X-linked.

Females who are heterozygous for these diseases are said to be carriers and may not exhibit any phenotypic effects. These females will pass the disease to half of their sons and will pass carrier status to half of their daughters; therefore, X-linked traits appear more frequently in males than females.

In some groups of organisms with sex chromosomes, the sex with the non-homologous sex chromosomes is the female rather than the male. This is the case for all birds. In this case, sex-linked traits will be more likely to appear in the female, in whom they are hemizygous.

Concept in Action



Watch [this video](#) to learn more about sex-linked traits.

The process of crossover, or recombination, occurs

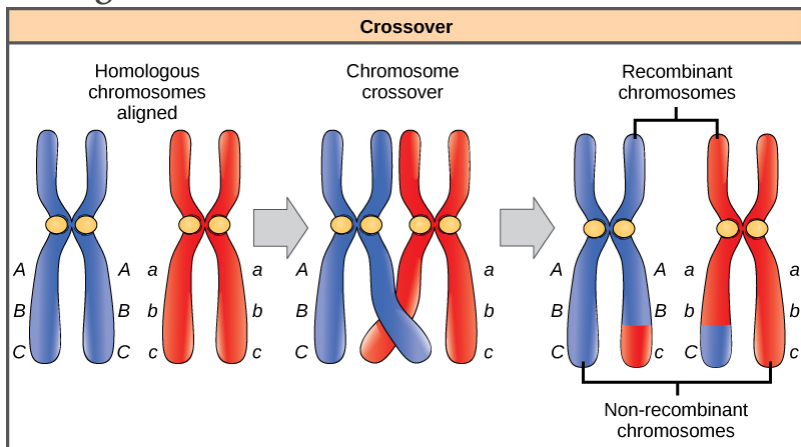
when two homologous chromosomes align and exchange a segment of genetic material.

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea plant characteristics behaved according to the law of independent assortment, we now know that some allele combinations are not inherited independently of each other. Genes that are located on separate, non-homologous chromosomes will always sort independently. However, each chromosome contains hundreds or thousands of genes, organized linearly on chromosomes like beads on a string. The segregation of alleles into gametes can be influenced by **linkage**, in which genes that are located physically close to each other on the same chromosome are more likely to be inherited as a pair. However, because of the process of recombination, or "crossover," it is possible for two genes on the same chromosome to behave independently, or as if they are not linked. To understand this, let us consider the biological basis of gene linkage and recombination.

Homologous chromosomes possess the same genes in the same order, though the specific alleles of the gene can be different on each of the two chromosomes. Recall that during interphase and prophase I of meiosis, homologous chromosomes

first replicate and then synapse, with like genes on the homologs aligning with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material ([link]). This process is called **recombination**, or crossover, and it is a common genetic process. Because the genes are aligned during recombination, the gene order is not altered. Instead, the result of recombination is that maternal and paternal alleles are combined onto the same chromosome. Across a given chromosome, several recombination events may occur, causing extensive shuffling of alleles.



When two genes are located on the same chromosome, they are considered linked, and their alleles tend to be transmitted through meiosis together. To exemplify this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has

alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will tend to go together into a gamete and the short and yellow alleles will go into other gametes. These are called the parental genotypes because they have been inherited intact from the parents of the individual producing gametes. But unlike if the genes were on different chromosomes, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create a Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes (the ones not like the parents) as a measure of how far apart genes are on a chromosome. Using this information, they have constructed linkage maps of genes on chromosomes for well-studied organisms, including humans.

Mendel's seminal publication makes no mention of linkage, and many researchers have questioned whether he encountered linkage but chose not to publish those crosses out of concern that they would invalidate his independent assortment postulate. The garden pea has seven chromosomes, and some

have suggested that his choice of seven characteristics was not a coincidence. However, even if the genes he examined were not located on separate chromosomes, it is possible that he simply did not observe linkage because of the extensive shuffling effects of recombination.

In this example of epistasis, one gene (C) masks the expression of another (A) for coat color. When the C allele is present, coat color is expressed; when it is absent (cc), no coat color is expressed. Coat color depends on the A gene, which shows dominance, with the recessive homozygote showing a different phenotype than the heterozygote or dominant homozygote.

Epistasis

Mendel's studies in pea plants implied that the sum of an individual's phenotype was controlled by genes (or as he called them, unit factors), such that every characteristic was distinctly and completely controlled by a single gene. In fact, single observable characteristics are almost always under the influence of multiple genes (each with two or more alleles) acting in unison. For example, at least eight genes contribute to eye color in humans.

Concept in Action



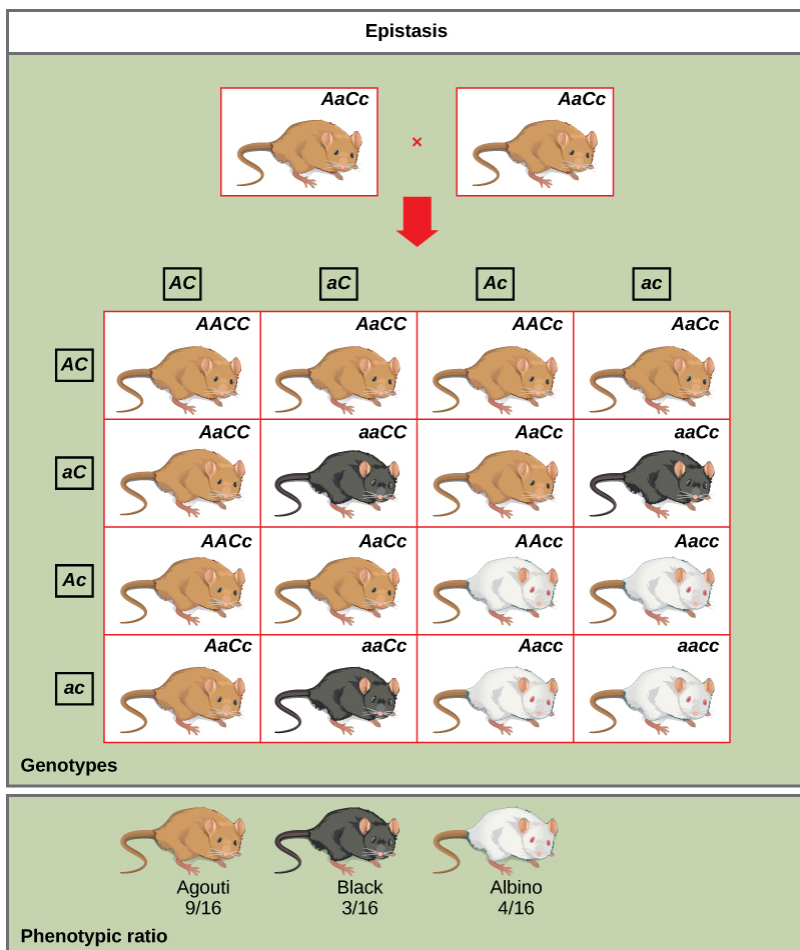
Eye color in humans is determined by multiple alleles. Use the [Eye Color Calculator](#) to predict the eye color of children from parental eye color.

In some cases, several genes can contribute to aspects of a common phenotype without their gene products ever directly interacting. In the case of organ development, for instance, genes may be expressed sequentially, with each gene adding to the complexity and specificity of the organ. Genes may function in complementary or synergistic fashions, such that two or more genes expressed simultaneously affect a phenotype. An apparent example of this occurs with human skin color, which appears to involve the action of at least three (and probably more) genes. Cases in which inheritance for a characteristic like skin color or human height depend on the combined effects of numerous genes are called polygenic inheritance.

Genes may also oppose each other, with one gene suppressing the expression of another. In **epistasis**, the interaction between genes is antagonistic, such

that one gene masks or interferes with the expression of another. “Epistasis” is a word composed of Greek roots meaning “standing upon.” The alleles that are being masked or silenced are said to be hypostatic to the epistatic alleles that are doing the masking. Often the biochemical basis of epistasis is a gene pathway in which expression of one gene is dependent on the function of a gene that precedes or follows it in the pathway.

An example of epistasis is pigmentation in mice. The wild-type coat color, agouti (AA) is dominant to solid-colored fur (aa). However, a separate gene C, when present as the recessive homozygote (cc), negates any expression of pigment from the A gene and results in an albino mouse ([\[link\]](#)). Therefore, the genotypes $AAcc$, $Aacc$, and $aacc$ all produce the same albino phenotype. A cross between heterozygotes for both genes ($AaCc \times AaCc$) would generate offspring with a phenotypic ratio of 9 agouti:3 black:4 albino ([\[link\]](#)). In this case, the C gene is epistatic to the A gene.



Section Summary

Alleles do not always behave in dominant and recessive patterns. Incomplete dominance describes situations in which the heterozygote exhibits a phenotype that is intermediate between the homozygous phenotypes. Codominance describes the simultaneous expression of both of the alleles in

the heterozygote. Although diploid organisms can only have two alleles for any given gene, it is common for more than two alleles for a gene to exist in a population. In humans, as in many animals and some plants, females have two X chromosomes and males have one X and one Y chromosome. Genes that are present on the X but not the Y chromosome are said to be X-linked, such that males only inherit one allele for the gene, and females inherit two.

According to Mendel's law of independent assortment, genes sort independently of each other into gametes during meiosis. This occurs because chromosomes, on which the genes reside, assort independently during meiosis and crossovers cause most genes on the same chromosomes to also behave independently. When genes are located in close proximity on the same chromosome, their alleles tend to be inherited together. This results in offspring ratios that violate Mendel's law of independent assortment. However, recombination serves to exchange genetic material on homologous chromosomes such that maternal and paternal alleles may be recombined on the same chromosome. This is why alleles on a given chromosome are not always inherited together. Recombination is a random event occurring anywhere on a chromosome. Therefore, genes that are far apart on the same chromosome are likely to still assort independently because of recombination

events that occurred in the intervening chromosomal space.

Whether or not they are sorting independently, genes may interact at the level of gene products, such that the expression of an allele for one gene masks or modifies the expression of an allele for a different gene. This is called epistasis.

Art Connections

[\[link\]](#) What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

[\[link\]](#) Half of the female offspring would be heterozygous ($X^W X^w$) with red eyes, and half would be homozygous recessive ($X^w X^w$) with white eyes. Half of the male offspring would be hemizygous dominant ($X^W Y$) with red eyes, and half would be hemizygous recessive ($X^w Y$) with white eyes.

Multiple Choice

If black and white true-breeding mice are mated and the result is all gray offspring, what inheritance pattern would this be indicative of?

1. dominance
 2. codominance
 3. multiple alleles
 4. incomplete dominance
-

D

The ABO blood groups in humans are expressed as the I_A , I_B , and i alleles. The I_A allele encodes the A blood group antigen, I_B encodes B, and i encodes O. Both A and B are dominant to O. If a heterozygous blood type A parent (I_Ai) and a heterozygous blood type B parent (I_Bi) mate, one quarter of their offspring are expected to have the AB blood type (I_AI_B) in which both antigens are expressed equally. Therefore, ABO blood groups are an example of:

1. multiple alleles and incomplete dominance
 2. codominance and incomplete dominance
 3. incomplete dominance only
 4. multiple alleles and codominance
-

D

In a cross between a homozygous red-eyed female fruit fly and a white-eyed male fruit fly, what is the expected outcome?

1. all white-eyed male offspring
2. all white-eyed female offspring
3. all red-eyed offspring
4. half white-eyed male offspring

C

When a population has a gene with four alleles circulating, how many possible genotypes are there?

1. 3
2. 6
3. 10
4. 16

C

Free Response

Can a male be a carrier of red-green color

blindness?

No, males can only express color blindness and cannot carry it because an individual needs two X chromosomes to be a carrier.

Could an individual with blood type O (genotype ii) be a legitimate child of parents in which one parent had blood type A and the other parent had blood type B?

Yes this child could have come from these parents. The child would have inherited an i allele from each parent and for this to happen the type A parent had to have genotype Iai and the type b parent had to have genotype Ibi .

Glossary

codominance

in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

epistasis

an interaction between genes such that one gene masks or interferes with the expression of another

hemizygous

the presence of only one allele for a characteristic, as in X-linkage; hemizygosity makes descriptions of dominance and recessiveness irrelevant

incomplete dominance

in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

linkage

a phenomenon in which alleles that are located in close proximity to each other on the same chromosome are more likely to be inherited together

recombination

the process during meiosis in which homologous chromosomes exchange linear segments of genetic material, thereby dramatically increasing genetic variation in the offspring and separating linked genes

wild type

the most commonly occurring genotype or phenotype for a given characteristic found in a population

X-linked

a gene present on the X chromosome, but not the Y chromosome

Prokaryotic Diversity

By the end of this section, you will be able to:

- Describe the evolutionary history of prokaryotes
- Discuss the distinguishing features of extremophiles
- Explain why it is difficult to culture prokaryotes

Prokaryotes are ubiquitous. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. In the typical human body, prokaryotic cells outnumber human body cells by about ten to one. They comprise the majority of living things in all ecosystems. Some prokaryotes thrive in environments that are inhospitable for most living things. Prokaryotes recycle **nutrients**—essential substances (such as carbon and nitrogen)—and they drive the evolution of new ecosystems, some of which are natural and others man-made.

Prokaryotes have been on Earth since long before multicellular life appeared.

This (a) microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the “Pacific Ring of Fire.” The mat helps retain microbial nutrients. Chimneys such as the one indicated by the arrow allow gases to escape. (b) In this micrograph, bacteria are visualized using fluorescence

microscopy. (credit a: modification of work by Dr. Bob Embley, NOAA PMEL, Chief Scientist; credit b: modification of work by Ricardo Murga, Rodney Donlan, CDC; scale-bar data from Matt Russell)(a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old. (credit a: Robert Young; credit b: P. Carrara, NPS) This hot spring in Yellowstone National Park flows toward the foreground. Cyanobacteria in the spring are green, and as water flows down the gradient, the intensity of the color increases as cell density increases. The water is cooler at the edges of the stream than in the center, causing the edges to appear greener. (credit: Graciela Brelles-Mariño)

Prokaryotes, the First Inhabitants of Earth

When and where did life begin? What were the conditions on Earth when life began? Prokaryotes were the first forms of life on Earth, and they existed for billions of years before plants and animals appeared. The Earth and its moon are thought to be about 4.54 billion years old. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from Earth and the moon. Early Earth had a very different atmosphere (contained less molecular oxygen) than it does today and was

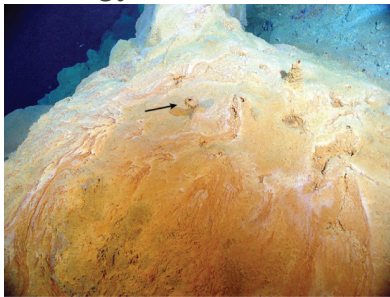
subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the Earth. At this time too, strong volcanic activity was common on Earth, so it is likely that these first organisms—the first prokaryotes—were adapted to very high temperatures. Early Earth was prone to geological upheaval and volcanic eruption, and was subject to bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

Microbial Mats

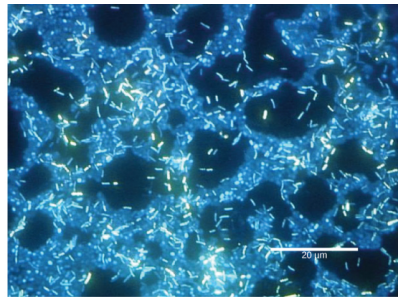
Microbial mats or large biofilms may represent the earliest forms of life on Earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A **microbial mat** is a multi-layered sheet of prokaryotes ([\[link\]](#)) that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, and they typically grow where different types of materials interface, mostly on moist surfaces. The various types of prokaryotes that comprise them carry out different metabolic pathways, and that is the reason for their various colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called extracellular matrix.

The first microbial mats likely obtained their energy

from chemicals found near hydrothermal vents. A **hydrothermal vent** is a breakage or fissure in the Earth's surface that releases geothermally heated water. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely available energy source—sunlight—whereas others were still dependent on chemicals from hydrothermal vents for energy and food.



(a)



(b)

Stromatolites

Fossilized microbial mats represent the earliest record of life on Earth. A **stromatolite** is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat ([\[link\]](#)). Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on Earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.



(a)



(b)

The Ancient Atmosphere

Evidence indicates that during the first two billion years of Earth's existence, the atmosphere was **anoxic**, meaning that there was no molecular oxygen. Therefore, only those organisms that can grow without oxygen—**anaerobic** organisms—were able to live. Autotrophic organisms that convert solar energy into chemical energy are called **phototrophs**, and they appeared within one billion years of the formation of Earth. Then, **cyanobacteria**, also known as blue-green algae, evolved from these simple phototrophs one billion years later. Cyanobacteria ([\[link\]](#)) began the oxygenation of the atmosphere. Increased atmospheric oxygen allowed the development of more efficient O₂-utilizing catabolic pathways. It also opened up the land to increased colonization, because some O₂ is converted into O₃ (ozone) and ozone effectively absorbs the ultraviolet light that would otherwise cause lethal mutations in DNA. Ultimately, the increase in O₂ concentrations allowed the evolution of other life forms.



Deinococcus radiodurans, visualized in this false color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has developed DNA repair mechanisms that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat. (credit: modification of work by Michael Daly; scale-bar data from Matt Russell) Bodaker, I, Itai, S, Suzuki, MT, Feingersh, R, Rosenberg, M, Maguire, ME, Shimshon, B, and others. Comparative community genomics in the Dead Sea: An increasingly extreme environment. *The ISME Journal* 4 (2010): 399–407, doi:10.1038/ismej.2009.141. published online 24 December 2009. (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats. (credit a: Julien Menichini; credit b:

NASA; scale-bar data from Matt Russell) In these agar plates, the growth medium is supplemented with red blood cells. Blood agar becomes transparent in the presence of hemolytic *Streptococcus*, which destroys red blood cells and is used to diagnose *Streptococcus* infections. The plate on the left is inoculated with non-hemolytic *Staphylococcus* (large white colonies), and the plate on the right is inoculated with hemolytic *Streptococcus* (tiny clear colonies). If you look closely at the right plate, you can see that the agar surrounding the bacteria has turned clear. (credit: Bill Branson, NCI)

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments: Some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall, a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria are able to form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, allow bacteria to be the most abundant life form in all terrestrial and aquatic

ecosystems.

Other bacteria and archaea are adapted to grow under extreme conditions and are called **extremophiles**, meaning “lovers of extremes.” Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Arctic and the Antarctic, in very dry places, deep inside Earth, in harsh chemical environments, and in high radiation environments ([\[link\]](#)), just to mention a few. These organisms give us a better understanding of prokaryotic diversity and open up the possibility of finding new prokaryotic species that may lead to the discovery of new therapeutic drugs or have industrial applications. Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles: They are identified based on the conditions in which they grow best, and several habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both alkaliphiles and halophiles ([\[link\]](#)). Other extremophiles, like **radioresistant** organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it ([\[link\]](#)).

Extremophiles and Their Preferred Conditions

Extremophile Type

Conditions for Optimal Growth

Acidophiles

pH 3 or below

Alkaliphiles

pH 9 or above

Thermophiles

Temperature 60–80 °C
(140–176 °F)

Hyperthermophiles

Temperature 80–122 °C
(176–250 °F)

Psychrophiles

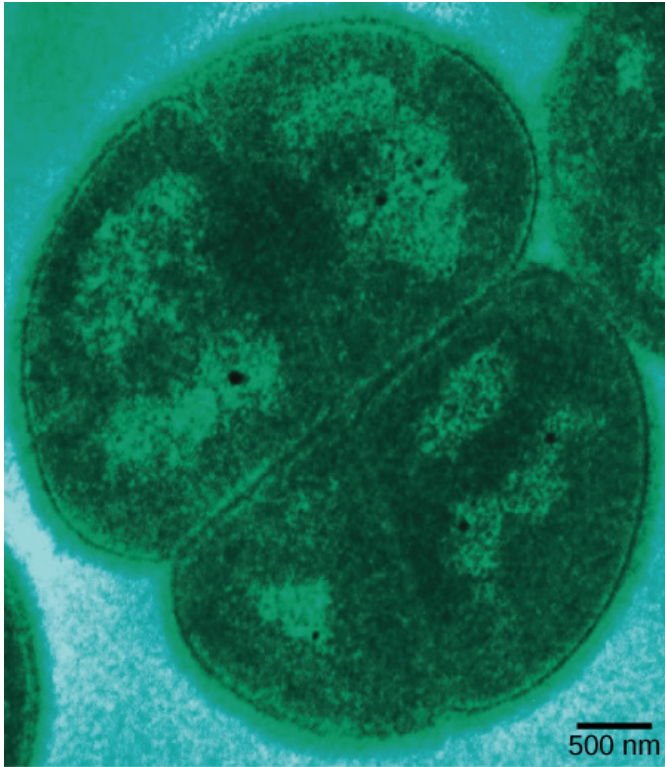
Temperature of -15–10 °C
(5–50 °F) or lower

Halophiles

Salt concentration of at
least 0.2 M

Osmophiles

High sugar concentration

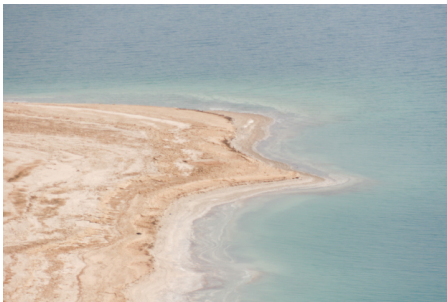


Prokaryotes in the Dead Sea

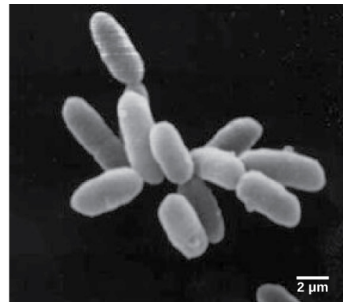
One example of a very harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. Hypersaline environments are essentially concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than that of seawater, and the water contains high levels of magnesium (about 40 times higher than in seawater) that would be toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+} , Ca^{2+} , and Mg^{2+}), produce what is commonly referred to as

“hard” water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and uniquely hostile, ecosystem^[footnote] ([\[link\]](#)).

What sort of prokaryotes do we find in the Dead Sea? The extremely salt-tolerant bacterial mats include *Halobacterium*, *Haloferax volcanii* (which is found in other locations, not only the Dead Sea), *Halorubrum sodomense*, and *Halobaculum gomorrense*, and the archaea *Haloarcula marismortui*, among others.



(a)



(b)

Unculturable Prokaryotes and the Viable-but-Non-Culturable State

Microbiologists typically grow prokaryotes in the laboratory using an appropriate culture medium containing all the nutrients needed by the target organism. The medium can be liquid, broth, or solid. After an incubation time at the right temperature, there should be evidence of microbial growth ([\[link\]](#)). The process of culturing bacteria is

complex and is one of the greatest discoveries of modern science. German physician Robert Koch is credited with discovering the techniques for pure culture, including staining and using growth media. His assistant Julius Petri invented the Petri dish whose use persists in today's laboratories. Koch worked primarily with the *Mycobacterium tuberculosis* bacterium that causes tuberculosis and developed postulates to identify disease-causing organisms that continue to be widely used in the medical community. Koch's postulates include that an organism can be identified as the cause of disease when it is present in all infected samples and absent in all healthy samples, and it is able to reproduce the infection after being cultured multiple times. Today, cultures remain a primary diagnostic tool in medicine and other areas of molecular biology.



Some prokaryotes, however, cannot grow in a laboratory setting. In fact, over 99 percent of

bacteria and archaea are unculturable. For the most part, this is due to a lack of knowledge as to what to feed these organisms and how to grow them; they have special requirements for growth that remain unknown to scientists, such as needing specific micronutrients, pH, temperature, pressure, co-factors, or co-metabolites. Some bacteria cannot be cultured because they are obligate intracellular parasites and cannot be grown outside a host cell.

In other cases, culturable organisms become unculturable under stressful conditions, even though the same organism could be cultured previously. Those organisms that cannot be cultured but are not dead are in a **viable-but-non-culturable** (VBNC) state. The VBNC state occurs when prokaryotes respond to environmental stressors by entering a dormant state that allows their survival. The criteria for entering into the VBNC state are not completely understood. In a process called **resuscitation**, the prokaryote can go back to “normal” life when environmental conditions improve.

Is the VBNC state an unusual way of living for prokaryotes? In fact, most of the prokaryotes living in the soil or in oceanic waters are non-culturable. It has been said that only a small fraction, perhaps one percent, of prokaryotes can be cultured under laboratory conditions. If these organisms are non-culturable, then how is it known whether they are present and alive? Microbiologists use molecular

techniques, such as the polymerase chain reaction (PCR), to amplify selected portions of DNA of prokaryotes, demonstrating their existence. Recall that PCR can make billions of copies of a DNA segment in a process called amplification.

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A **biofilm** is a microbial community ([\[link\]](#)) held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described as well as some composed of a mixture of fungi and bacteria.

Biofilms are present almost everywhere: they can cause the clogging of pipes and readily colonize surfaces in industrial settings. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of

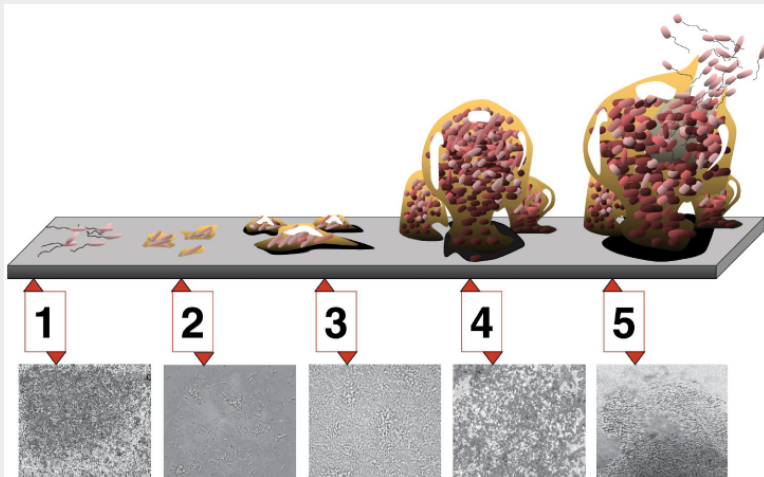
our teeth.

Interactions among the organisms that populate a biofilm, together with their protective exopolysaccharidic (EPS) environment, make these communities more robust than free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

Art Connection

Five stages of biofilm development are shown. During stage 1, initial attachment, bacteria adhere to a solid surface via weak van der Waals interactions. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the bacteria to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other bacteria. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the biofilm matrix is partly broken down, allowing some bacteria to

escape and colonize another surface. Micrographs of a *Pseudomonas aeruginosa* biofilm in each of the stages of development are shown. (credit: D. Davis, Don Monroe, PLoS)



Compared to free-floating bacteria, bacteria in biofilms often show increased resistance to antibiotics and detergents. Why do you think this might be the case?

Section Summary

Prokaryotes existed for billions of years before plants and animals appeared. Hot springs and hydrothermal vents may have been the environments in which life began. Microbial mats are thought to represent the earliest forms of life on

Earth, and there is fossil evidence of their presence about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that grows at interfaces between different types of material, mostly on moist surfaces. During the first 2 billion years, the atmosphere was anoxic and only anaerobic organisms were able to live.

Cyanobacteria evolved from early phototrophs and began the oxygenation of the atmosphere. The increase in oxygen concentration allowed the evolution of other life forms. Fossilized microbial mats are called stromatolites and consist of laminated organo-sedimentary structures formed by precipitation of minerals by prokaryotes. They represent the earliest fossil record of life on Earth.

Bacteria and archaea grow in virtually every environment. Those that survive under extreme conditions are called extremophiles (extreme lovers). Some prokaryotes cannot grow in a laboratory setting, but they are not dead. They are in the viable-but-non-culturable (VBNC) state. The VBNC state occurs when prokaryotes enter a dormant state in response to environmental stressors. Most prokaryotes are social and prefer to live in communities where interactions take place. A biofilm is a microbial community held together in a gummy-textured matrix.

Art Connections

[\[link\]](#) Compared to free-floating bacteria, bacteria in biofilms often show increased resistance to antibiotics and detergents. Why do you think this might be the case?

[\[link\]](#) The extracellular matrix and outer layer of cells protects the inner bacteria. The close proximity of cells also facilitates lateral gene transfer, a process by which genes such as antibiotic resistance genes are transferred from one bacterium to another. And even if lateral gene transfer does not occur, one bacterium that produces an exo-enzyme that destroys antibiotic may save neighboring bacteria.

Review Questions

The first forms of life on Earth were thought to be_____.

1. single-celled plants
 2. prokaryotes
 3. insects
 4. large animals such as dinosaurs
-

A

Microbial mats _____.

1. are the earliest forms of life on Earth
2. obtained their energy and food from hydrothermal vents
3. are multi-layered sheet of prokaryotes including mostly bacteria but also archaea
4. all of the above

D

The first organisms that oxygenated the atmosphere were

1. cyanobacteria
2. phototrophic organisms
3. anaerobic organisms
4. all of the above

A

Halophiles are organisms that require_____.

1. a salt concentration of at least 0.2 M
2. high sugar concentration

- 3. the addition of halogens
 - 4. all of the above
-

A

Free Response

Describe briefly how you would detect the presence of a non-culturable prokaryote in an environmental sample.

As the organisms are non-culturable, the presence could be detected through molecular techniques, such as PCR.

Why do scientists believe that the first organisms on Earth were extremophiles?

Because the environmental conditions on Earth were extreme: high temperatures, lack of oxygen, high radiation, and the like.

Glossary

acidophile

organism with optimal growth pH of three or below

alkaliphile

organism with optimal growth pH of nine or above

anaerobic

refers to organisms that grow without oxygen

anoxic

without oxygen

biofilm

a microbial community growing together on a surface, often held together with a gummy matrix

cyanobacteria

bacteria that evolved from early phototrophs and oxygenated the atmosphere; also known as blue-green algae

extremophile

organism that grows under extreme or harsh conditions

halophile

organism that require a salt concentration of at least 0.2 M

hydrothermal vent

fissure in Earth's surface that releases geothermally heated water

hyperthermophile

organism that grows at temperatures between 80–122 °C

microbial mat

multi-layered sheet of prokaryotes that may include bacteria and archaea

nutrient

essential substances for growth, such as carbon and nitrogen

osmophile

organism that grows in a high sugar concentration

phototroph

organism that is able to make its own food by converting solar energy to chemical energy

psychrophile

organism that grows at temperatures of -15 °C or lower

radioresistant

organism that grows in high levels of radiation

resuscitation

process by which prokaryotes that are in the

VBNC state return to viability

stromatolite

layered sedimentary structure formed by precipitation of minerals by prokaryotes in microbial mats

thermophile

organism that lives at temperatures between 60–80 °C

viable-but-non-culturable (VBNC) state

survival mechanism of bacteria facing environmental stress conditions

Eukaryotic Origins

By the end of this section, you will be able to:

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain endosymbiotic theory

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils found appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 μm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 μm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor, because these characteristics are present in at least some of the members of each major lineage.

1. Cells with nuclei surrounded by a nuclear envelope with nuclear pores. This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. Mitochondria. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but they are descended from ancestors that possessed them.

5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sex, a process of genetic recombination unique to eukaryotes in which diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei and subsequent karyogamy, a stage where two haploid nuclei fuse together to create a diploid zygote nucleus.
8. Members of all major lineages have cell walls, and it might be reasonable to conclude that the last common ancestor could make cell walls during some stage of its life cycle. However, not enough is known about eukaryotes' cell walls and their development to know how much homology exists among them. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

(a) This chloroplast cross-section illustrates its

elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell) (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Endosymbiosis and the Evolution of Eukaryotes

In order to understand eukaryotic organisms fully, it is necessary to understand that all extant eukaryotes are descendants of a chimeric organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that “took up residence” inside it. This major theme in the origin of eukaryotes is known as **endosymbiosis**, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms

that depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes ([\[link\]](#)). Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in prokaryotes, and some of these, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and many forms of evidence suggest that such anaerobic prokaryotes never carried out aerobic respiration nor did their ancestors.

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that it originally lacked O_2 . Without oxygen, aerobic respiration would not be expected, and living things would have relied on fermentation instead. At some point before, about 3.5 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen,

derived from various sources, was captured using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms, since it can damage many organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they appeared as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late

1800s, where they appeared to be somewhat worm-shaped structures that seemed to be moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration. In the 1960s, American biologist Lynn Margulis developed **endosymbiotic theory**, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such. In 1967, Margulis introduced new work on the theory and substantiated her findings through microbiological evidence. Although Margulis' work initially was met with resistance, this once-revolutionary hypothesis is now widely (but not completely) accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved. Much still remains to be discovered about the origins of the cells that now make up the cells in all living eukaryotes.

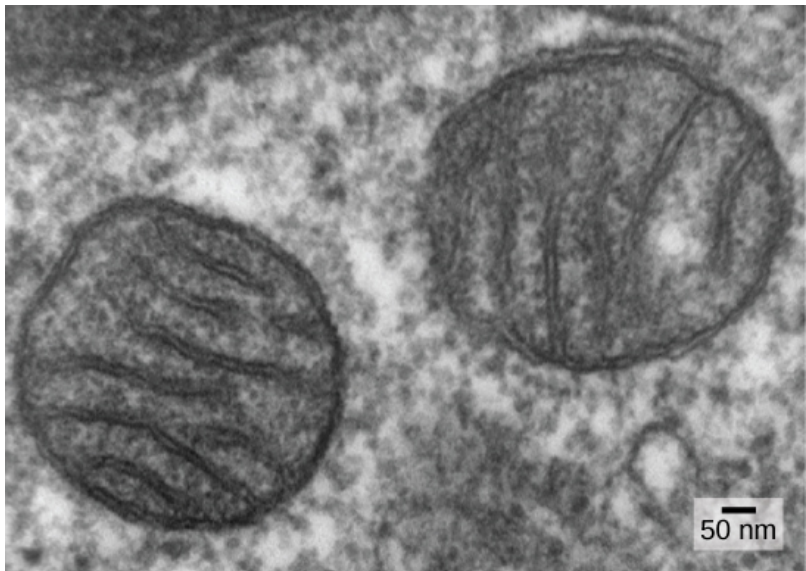
Broadly, it has become clear that many of our

nuclear genes and the molecular machinery responsible for replication and expression appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched ([\[link\]](#)). Mitochondria arise from the division of existing mitochondria; they may fuse together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by

photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support that mitochondria are derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.



Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (*de novo*) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living

prokaryotes.

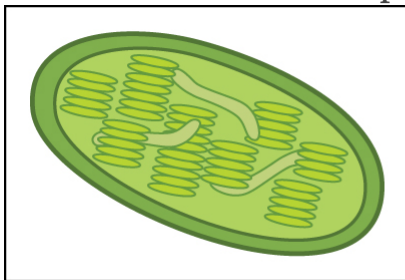
Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin. In addition

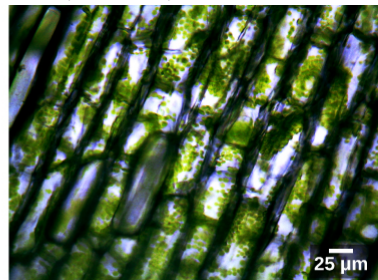
to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. Therefore, most biologists accept that the last common ancestor of eukaryotes had mitochondria.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a **plastid**. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called accessory pigments, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts ([\[link\]](#)).



(a)



(b)

Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also

championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. The best evidence is that this has happened twice in the history of eukaryotes. In one case, the common ancestor of the major lineage/supergroup Archaeplastida took on a cyanobacterial endosymbiont; in the other, the ancestor of the small amoeboid rhizarian taxon, *Paulinella*, took on a different cyanobacterial endosymbiont. Almost all photosynthetic eukaryotes are descended from the first event, and only a couple of species are derived from the other.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis. Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

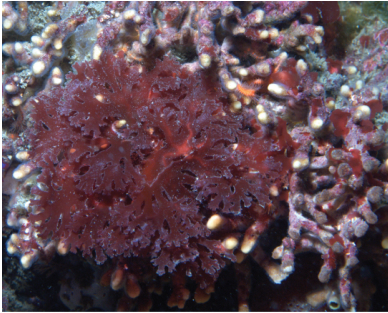
Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. Each chloroplast is surrounded by two membranes. In the group of Archaeplastida called the glaucophytes and in

Paulinella, a thin peptidoglycan layer is present between the outer and inner plastid membranes. All other plastids lack this relictual cyanobacterial wall. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to Archaeplastida occurred 1 to 1.5 billion years ago, at least 5 hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from Archaeplastida) as endosymbionts ([\[link\]](#)**ab**). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus of endosymbiotic alga.

Others have not “kept” any remnants. There are cases where tertiary or higher-order endosymbiotic events are the best explanations for plastids in some eukaryotes.



(a)



(b)

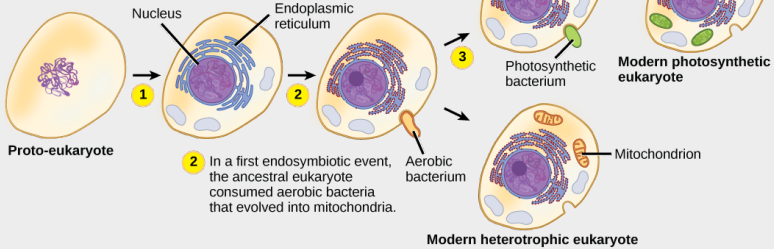
Art Connection

The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

The ENDOSYMBIOTIC THEORY

1 Infoldings in the plasma membrane of an ancestral prokaryote gave rise to endomembrane components, including a nucleus and endoplasmic reticulum.

3 In a second endosymbiotic event, the early eukaryote consumed photosynthetic bacteria that evolved into chloroplasts.



What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Evolution Connection

Secondary Endosymbiosis in Chlorarachniophytes

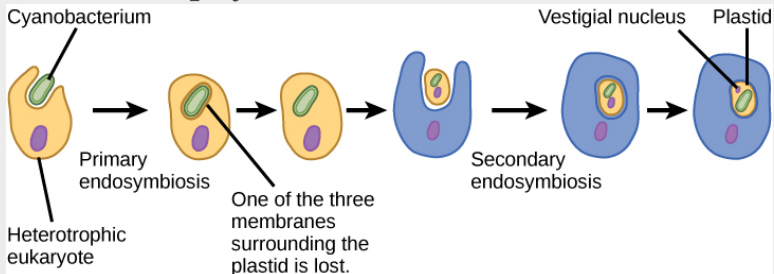
Endosymbiosis involves one cell engulfing another to produce, over time, a coevolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote.

This leads to the question of the possibility of a cell containing an endosymbiont to itself become engulfed, resulting in a secondary endosymbiosis. Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event.

Chlorarachniophytes are rare algae indigenous to

tropical seas and sand that can be classified into the rhizarian supergroup. Chlorarachniophytes extend thin cytoplasmic strands, interconnecting themselves with other chlorarachniophytes, in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium ([\[link\]](#)).

The hypothesized process of endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.



Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it

appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only three membranes can be identified around plastids. This is currently rectified as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

Section Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's

eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

Art Connections

[\[link\]](#) What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

[\[link\]](#) All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Review Questions

What event is thought to have contributed to the evolution of eukaryotes?

1. global warming
 2. glaciation
 3. volcanic activity
 4. oxygenation of the atmosphere
-

D

Which characteristic is shared by prokaryotes and eukaryotes?

1. cytoskeleton
 2. nuclear envelope
 3. DNA-based genome
 4. mitochondria
-

C

Mitochondria most likely evolved by _____.

1. a photosynthetic cyanobacterium
 2. cytoskeletal elements
 3. endosymbiosis
 4. membrane proliferation
-

C

Which of these protists is believed to have evolved following a secondary endosymbiosis?

1. green algae
 2. cyanobacteria
 3. red algae
 4. chlorarachniophytes
-

D

Free Response

Describe the hypothesized steps in the origin of eukaryotic cells.

Eukaryotic cells arose through endosymbiotic events that gave rise to the energy-producing organelles within the eukaryotic cells such as

mitochondria and chloroplasts. The nuclear genome of eukaryotes is related most closely to the Archaea, so it may have been an early archaean that engulfed a bacterial cell that evolved into a mitochondrion. Mitochondria appear to have originated from an alpha-proteobacterium, whereas chloroplasts originated as a cyanobacterium. There is also evidence of secondary endosymbiotic events. Other cell components may also have resulted from endosymbiotic events.

Glossary

endosymbiosis

engulfment of one cell within another such that the engulfed cell survives, and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

endosymbiotic theory

theory that states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such

plastid

one of a group of related organelles in plant cells that are involved in the storage of

starches, fats, proteins, and pigments

The Evolutionary History of the Animal Kingdom

By the end of this section, you will be able to:

- Describe the features that characterized the earliest animals and when they appeared on earth
- Explain the significance of the Cambrian period for animal evolution and the changes in animal diversity that took place during that time
- Describe some of the unresolved questions surrounding the Cambrian explosion
- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

Many questions regarding the origins and evolutionary history of the animal kingdom continue to be researched and debated, as new fossil and molecular evidence change prevailing theories. Some of these questions include the following: How long have animals existed on Earth? What were the earliest members of the animal kingdom, and what organism was their common ancestor? While animal diversity increased during the Cambrian period of the Paleozoic era, 530 million years ago, modern fossil evidence suggests that primitive animal species existed much earlier.

(a) Earth's history is divided into eons, eras, and periods. Note that the Ediacaran period starts in the Proterozoic eon and ends in the Cambrian period of the Phanerozoic eon. (b) Stages on the geological

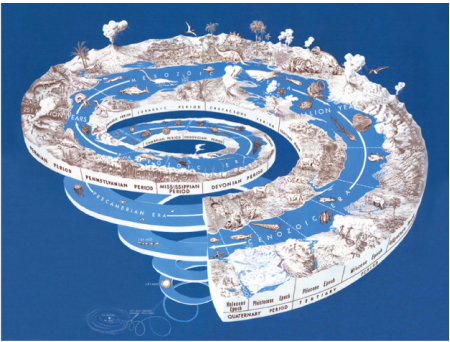
time scale are represented as a spiral. (credit: modification of work by USGS)Fossils of (a) *Cyclomedusa* and (b) *Dickinsonia* date to 650 million years ago, during the Ediacaran period. (credit: modification of work by “Smith609”/Wikimedia Commons)

Pre-Cambrian Animal Life

The time before the Cambrian period is known as the **Ediacaran period** (from about 635 million years ago to 543 million years ago), the final period of the late Proterozoic Neoproterozoic Era ([\[link\]](#)). It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protist species called choanoflagellates closely resemble the choanocyte cells in the simplest animals, sponges. In addition to their morphological similarity, molecular analyses have revealed similar sequence homologies in their DNA.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	1.6
		Tertiary	66
		Cretaceous	138
	Mesozoic	Jurassic	205
		Triassic	240
		Permian	290
	Paleozoic	Pennsylvanian	330
		Mississippian	360
		Devonian	410
		Silurian	435
		Ordovician	500
		Cambrian	540
	Proterozoic	Ediacaran	635-543 MYA
Archean	Late Proterozoic		
	Middle Proterozoic		
	Early Proterozoic		2500
Pre-Archean			3800?

(a)



(b)

The earliest life comprising Ediacaran biota was long believed to include only tiny, sessile, soft-

bodied sea creatures. However, recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and possibly even before the Ediacaran period.

Fossils believed to represent the oldest animals with hard body parts were recently discovered in South Australia. These sponge-like fossils, named *Coronacollina acula*, date back as far as 560 million years, and are believed to show the existence of hard body parts and spicules that extended 20–40 cm from the main body (estimated about 5 cm long). Other fossils from the Ediacaran period are shown in [\[link\]](#)ab.



(a)



(b)

Another recent fossil discovery may represent the earliest animal species ever found. While the validity of this claim is still under investigation, these primitive fossils appear to be small, one-centimeter long, sponge-like creatures. These fossils from South Australia date back 650 million years, actually placing the putative animal before the great

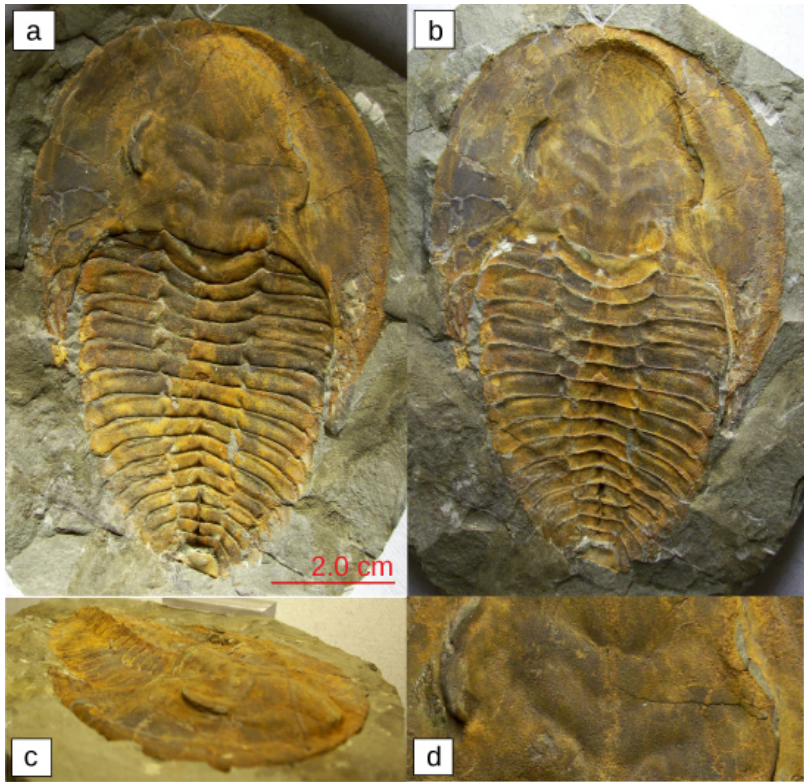
ice age extinction event that marked the transition between the **Cryogenian period** and the Ediacaran period. Until this discovery, most scientists believed that there was no animal life prior to the Ediacaran period. Many scientists now believe that animals may in fact have evolved during the Cryogenian period.

An artist's rendition depicts some organisms from the Cambrian period. These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago. The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

The Cambrian Explosion of Animal Life

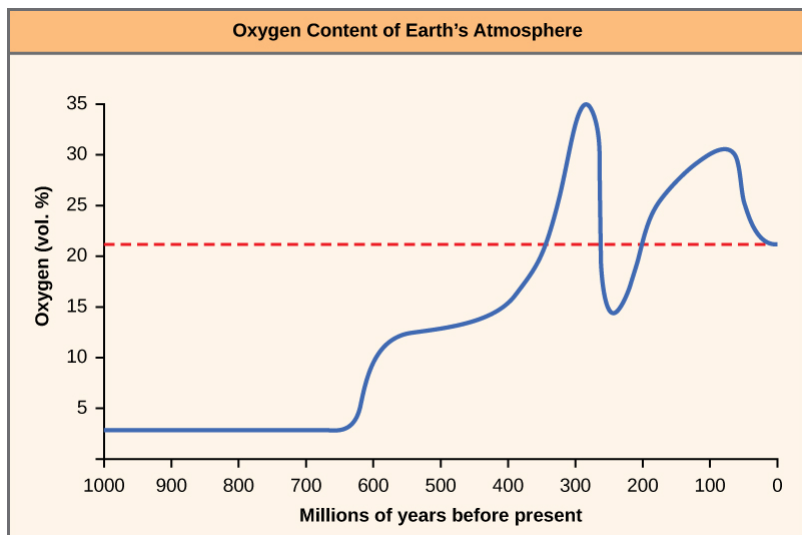
The Cambrian period, occurring between approximately 542–488 million years ago, marks the most rapid evolution of new animal phyla and animal diversity in Earth's history. It is believed that most of the animal phyla in existence today had their origins during this time, often referred to as the **Cambrian explosion** ([\[link\]](#)). Echinoderms, mollusks, worms, arthropods, and chordates arose during this period. One of the most dominant species during the Cambrian period was the trilobite, an arthropod that was among the first animals to exhibit a sense of vision ([\[link\]](#)[abcd](#)).





The cause of the Cambrian explosion is still debated. There are many theories that attempt to answer this question. Environmental changes may have created a more suitable environment for animal life. Examples of these changes include rising atmospheric oxygen levels and large increases in oceanic calcium concentrations that preceded the Cambrian period ([\[link\]](#)). Some scientists believe that an expansive, continental shelf with numerous shallow lagoons or pools provided the necessary living space for larger numbers of different types of animals to co-exist. There is also support for theories that argue that ecological relationships

between species, such as changes in the food web, competition for food and space, and predator-prey relationships, were primed to promote a sudden massive coevolution of species. Yet other theories claim genetic and developmental reasons for the Cambrian explosion. The morphological flexibility and complexity of animal development afforded by the evolution of *Hox* control genes may have provided the necessary opportunities for increases in possible animal morphologies at the time of the Cambrian period. Theories that attempt to explain why the Cambrian explosion happened must be able to provide valid reasons for the massive animal diversification, as well as explain why it happened *when* it did. There is evidence that both supports and refutes each of the theories described above, and the answer may very well be a combination of these and other theories.



However, unresolved questions about the animal diversification that took place during the Cambrian period remain. For example, we do not understand how the evolution of so many species occurred in such a short period of time. Was there really an “explosion” of life at this particular time? Some scientists question the validity of this idea, because there is increasing evidence to suggest that more animal life existed prior to the Cambrian period and that other similar species’ so-called explosions (or radiations) occurred later in history as well. Furthermore, the vast diversification of animal species that appears to have begun during the Cambrian period continued well into the following Ordovician period. Despite some of these arguments, most scientists agree that the Cambrian period marked a time of impressively rapid animal evolution and diversification that is unmatched elsewhere during history.

Link to Learning



View an animation of what ocean life may have been like during the Cambrian explosion.

https://www.openstaxcollege.org/l/ocean_life

Mass extinctions have occurred repeatedly over geological time.

Post-Cambrian Evolution and Mass Extinctions

The periods that followed the Cambrian during the Paleozoic Era are marked by further animal evolution and the emergence of many new orders, families, and species. As animal phyla continued to diversify, new species adapted to new ecological niches. During the Ordovician period, which followed the Cambrian period, plant life first appeared on land. This change allowed formerly aquatic animal species to invade land, feeding directly on plants or decaying vegetation. Continual changes in temperature and moisture throughout the remainder of the Paleozoic Era due to continental plate movements encouraged the development of new adaptations to terrestrial existence in animals, such as limbed appendages in amphibians and epidermal scales in reptiles.

Changes in the environment often create new niches (living spaces) that contribute to rapid speciation

and increased diversity. On the other hand, cataclysmic events, such as volcanic eruptions and meteor strikes that obliterate life, can result in devastating losses of diversity. Such periods of **mass extinction** ([\[link\]](#)) have occurred repeatedly in the evolutionary record of life, erasing some genetic lines while creating room for others to evolve into the empty niches left behind. The end of the Permian period (and the Paleozoic Era) was marked by the largest mass extinction event in Earth's history, a loss of roughly 95 percent of the extant species at that time. Some of the dominant phyla in the world's oceans, such as the trilobites, disappeared completely. On land, the disappearance of some dominant species of Permian reptiles made it possible for a new line of reptiles to emerge, the dinosaurs. The warm and stable climatic conditions of the ensuing Mesozoic Era promoted an explosive diversification of dinosaurs into every conceivable niche in land, air, and water. Plants, too, radiated into new landscapes and empty niches, creating complex communities of producers and consumers, some of which became very large on the abundant food available.

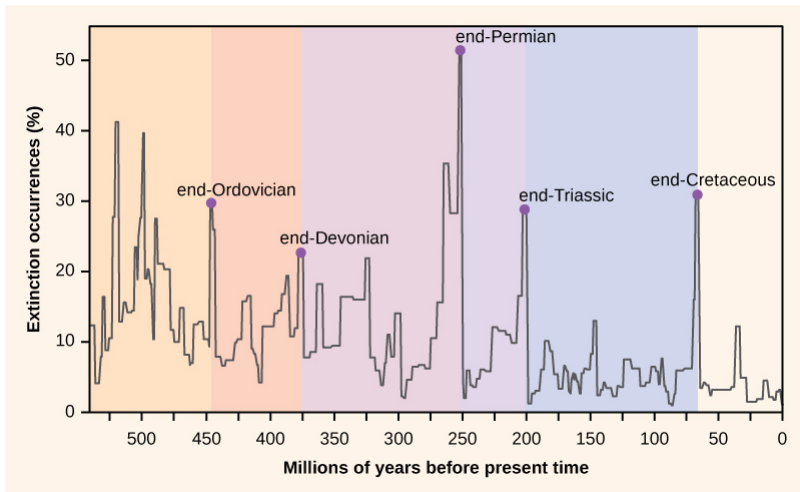
Another mass extinction event occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end. Skies darkened and temperatures fell as a large meteor impact and tons of volcanic ash blocked incoming sunlight. Plants died, herbivores and carnivores starved, and the mostly cold-blooded

dinosaurs ceded their dominance of the landscape to more warm-blooded mammals. In the following Cenozoic Era, mammals radiated into terrestrial and aquatic niches once occupied by dinosaurs, and birds, the warm-blooded offshoots of one line of the ruling reptiles, became aerial specialists. The appearance and dominance of flowering plants in the Cenozoic Era created new niches for insects, as well as for birds and mammals. Changes in animal species diversity during the late Cretaceous and early Cenozoic were also promoted by a dramatic shift in Earth's geography, as continental plates slid over the crust into their current positions, leaving some animal groups isolated on islands and continents, or separated by mountain ranges or inland seas from other competitors. Early in the Cenozoic, new ecosystems appeared, with the evolution of grasses and coral reefs. Late in the Cenozoic, further extinctions followed by speciation occurred during ice ages that covered high latitudes with ice and then retreated, leaving new open spaces for colonization.

Link to Learning



Watch the following [video](#) to learn more about the mass extinctions.



Career Connection

Paleontologist

Natural history museums contain the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontologists are scientists who study prehistoric life. They use

fossils to observe and explain how life evolved on Earth and how species interacted with each other and with the environment. A paleontologist needs to be knowledgeable in biology, ecology, chemistry, geology, and many other scientific disciplines. A paleontologist's work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

Section Summary

The most rapid diversification and evolution of animal species in all of history occurred during the Cambrian period of the Paleozoic Era, a phenomenon known as the Cambrian explosion.

Until recently, scientists believed that there were only very few tiny and simplistic animal species in existence before this period. However, recent fossil discoveries have revealed that additional, larger, and more complex animals existed during the Ediacaran period, and even possibly earlier, during the Cryogenian period. Still, the Cambrian period undoubtedly witnessed the emergence of the majority of animal phyla that we know today, although many questions remain unresolved about this historical phenomenon.

The remainder of the Paleozoic Era is marked by the growing appearance of new classes, families, and species, and the early colonization of land by certain marine animals. The evolutionary history of animals is also marked by numerous major extinction events, each of which wiped out a majority of extant species. Some species of most animal phyla survived these extinctions, allowing the phyla to persist and continue to evolve into species that we see today.

Review Questions

Which of the following periods is the earliest during which animals may have appeared?

1. Ordovician period

2. Cambrian period
 3. Ediacaran period
 4. Cryogenian period
-

D

What type of data is primarily used to determine the existence and appearance of early animal species?

1. molecular data
 2. fossil data
 3. morphological data
 4. embryological development data
-

B

The time between 542–488 million years ago marks which period?

1. Cambrian period
 2. Silurian period
 3. Ediacaran period
 4. Devonian period
-

A

Until recent discoveries suggested otherwise, animals existing before the Cambrian period were believed to be:

1. small and ocean-dwelling
 2. small and non-motile
 3. small and soft-bodied
 4. small and radially symmetrical or asymmetrical
-

C

Plant life first appeared on land during which of the following periods?

1. Cambrian period
 2. Ordovician period
 3. Silurian period
 4. Devonian period
-

B

Approximately how many mass extinction events occurred throughout the evolutionary history of animals?

1. 3
2. 4

3. 5

4. more than 5

D

Free Response

Briefly describe at least two theories that attempt to explain the cause of the Cambrian explosion.

One theory states that environmental factors led to the Cambrian explosion. For example, the rise in atmospheric oxygen and oceanic calcium levels helped to provide the right environmental conditions to allow such a rapid evolution of new animal phyla. Another theory states that ecological factors such as competitive pressures and predator-prey relationships reached a threshold that supported the rapid animal evolution that took place during the Cambrian period.

How is it that most, if not all, of the extant animal phyla today evolved during the

Cambrian period if so many massive extinction events have taken place since then?

It is true that multiple mass extinction events have taken place since the Cambrian period, when most currently existing animal phyla appeared, and the majority of animal species were commonly wiped out during these events. However, a small number of animal species representing each phylum were usually able to survive each extinction event, allowing the phylum to continue to evolve rather than become altogether extinct.

Glossary

Cambrian explosion

time during the Cambrian period (542–488 million years ago) when most of the animal phyla in existence today evolved

Cryogenian period

geologic period (850–630 million years ago) characterized by a very cold global climate

Ediacaran period

geological period (630–542 million years ago) when the oldest definite multicellular organisms with tissues evolved

mass extinction

event that wipes out the majority of species
within a relatively short geological time
period

Population Evolution

By the end of this section, you will be able to:

- Define population genetics and describe how population genetics is used in the study of the evolution of populations
- Define the Hardy-Weinberg principle and discuss its importance

The mechanisms of inheritance, or genetics, were not understood at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to understanding many aspects of evolution. In fact, the predominant (and incorrect) genetic theory of the time, blending inheritance, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of Darwin's book, *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the **modern synthesis**—the coherent understanding of the relationship between natural

selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary processes, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this change of a population over time, called **microevolution**, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called **macroevolution**.

Everyday Connection

Evolution and Flu Vaccines

Every fall, the media starts reporting on flu vaccinations and potential outbreaks. Scientists, health experts, and institutions determine recommendations for different parts of the population, predict optimal production and inoculation schedules, create vaccines, and set up clinics to provide inoculations. You may think of the annual flu shot as a lot of media hype, an important health protection, or just a briefly uncomfortable prick in your arm. But do you think of it in terms of evolution?

The media hype of annual flu shots is scientifically grounded in our understanding of evolution. Each year, scientists across the globe strive to predict the flu strains that they anticipate being most

widespread and harmful in the coming year. This knowledge is based in how flu strains have evolved over time and over the past few flu seasons.

Scientists then work to create the most effective vaccine to combat those selected strains. Hundreds of millions of doses are produced in a short period in order to provide vaccinations to key populations at the optimal time.

Because viruses, like the flu, evolve very quickly (especially in evolutionary time), this poses quite a challenge. Viruses mutate and replicate at a fast rate, so the vaccine developed to protect against last year's flu strain may not provide the protection needed against the coming year's strain. Evolution of these viruses means continued adaptations to ensure survival, including adaptations to survive previous vaccines.

Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58.

Population Genetics

Recall that a gene for a particular character may have several alleles, or variants, that code for different traits associated with that character. For

example, in the ABO blood type system in humans, three alleles determine the particular blood-type carbohydrate on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists in a field of study known as **population genetics** began to study how selective forces change a population through changes in allele and genotypic frequencies.

The **allele frequency** (or gene frequency) is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, the term evolution is defined as a change in the frequency of an allele in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, I_A , is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan^[footnote] found a frequency of I_A to be 26.1 percent. The I_B and I_O alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies added up to 100 percent. A change in this frequency over time would constitute evolution

in the population.

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the process of natural selection. Natural selection can alter the population's genetic makeup; for example, if a given allele confers a phenotype that allows an individual to better survive or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus, perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The **gene pool** is the sum of all the alleles in a population.

Sometimes, allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies. This phenomenon is called genetic drift. Natural selection and genetic drift usually occur simultaneously in populations and are not isolated events. It is hard to determine which process dominates because it is often nearly impossible to determine the cause of change in allele frequencies

at each occurrence. An event that initiates an allele frequency change in an isolated part of the population, which is not typical of the original population, is called the **founder effect**. Natural selection, random drift, and founder effects can lead to significant changes in the genome of a population.

Hardy-Weinberg Principle of Equilibrium

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the genetic makeup of a population. The theory, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population's allele and genotype frequencies are inherently stable— unless some kind of evolutionary force is acting upon the population, neither the allele nor the genotypic frequencies would change. The Hardy-Weinberg principle assumes conditions with no mutations, migration, emigration, or selective pressure for or against genotype, plus an infinite population; while no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes.

Working under this theory, population geneticists represent different alleles as different variables in

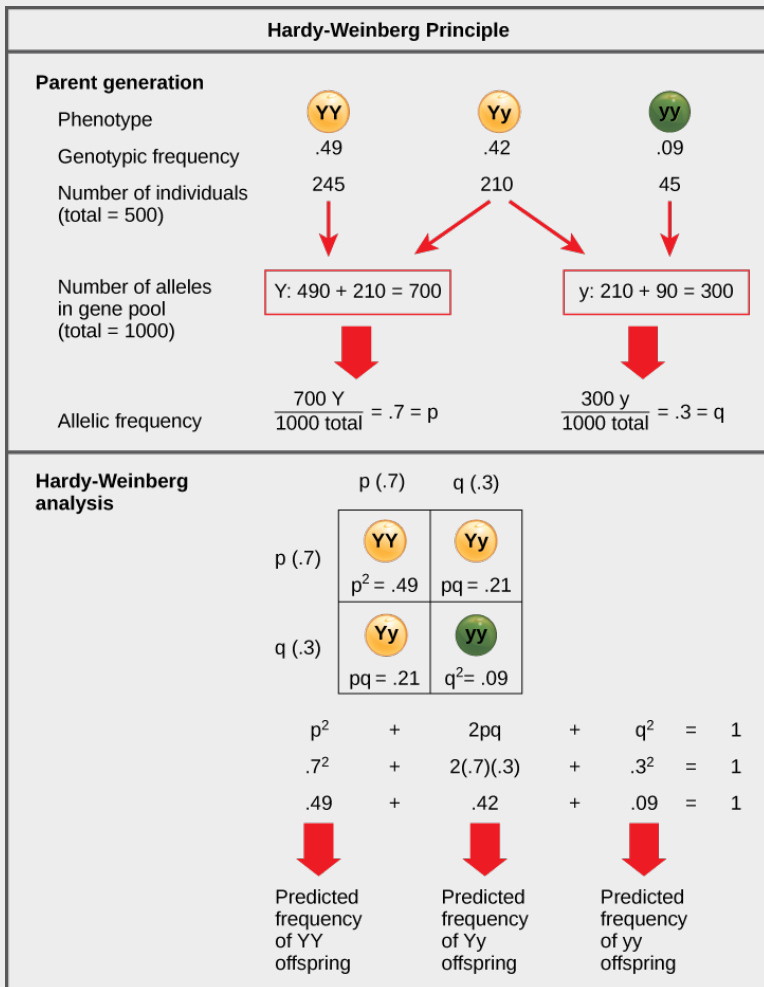
their mathematical models. The variable p , for example, often represents the frequency of a particular allele, say Y for the trait of yellow in Mendel's peas, while the variable q represents the frequency of y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, $p + q = 1$. In other words, all the p alleles and all the q alleles make up all of the alleles for that locus that are found in the population.

But what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, known as the population's **genetic structure**, from which scientists can surmise the distribution of phenotypes. If the phenotype is observed, only the genotype of the homozygous recessive alleles can be known; the calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if the allele frequencies (p and q) are known, predicting the frequencies of these genotypes is a simple mathematical calculation to determine the probability of getting these genotypes if two alleles are drawn at random from the gene pool. So in the above scenario, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus producing green peas ([link](#)). In other words, the frequency of pp individuals is simply p^2 ; the frequency of pq individuals is $2pq$; and the

frequency of qq individuals is q^2 . And, again, if p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

Art Connection

When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined from the Hardy-Weinberg equation. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.



In plants, violet flower color (V) is dominant over white (v). If $p = 0.8$ and $q = 0.2$ in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

In theory, if a population is at equilibrium—that is, there are no evolutionary forces acting upon it—generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all of the time. Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. But the Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

Link to Learning



Use this [online calculator](#) to determine the genetic structure of a population.

Section Summary

The modern synthesis of evolutionary theory grew out of the cohesion of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity, along with the more modern study of population genetics. It describes the evolution of populations and species, from small-scale changes among individuals to large-scale changes over paleontological time periods. To understand how organisms evolve, scientists can track populations' allele frequencies over time. If they differ from generation to generation, scientists can conclude that the population is not in Hardy-Weinberg equilibrium, and is thus evolving.

Art Connections

[\[link\]](#) In plants, violet flower color (V) is dominant over white (v). If $p = .8$ and $q = 0.2$ in a population of 500 plants, how many

individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

[\[link\]](#) The expected distribution is 320 VV, 160Vv, and 20 vv plants. Plants with VV or Vv genotypes would have violet flowers, and plants with the vv genotype would have white flowers, so a total of 480 plants would be expected to have violet flowers, and 20 plants would have white flowers.

Review Questions

What is the difference between micro- and macroevolution?

1. Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
2. Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.

3. Microevolution describes the evolution of organisms in populations, while macroevolution describes the evolution of species over long periods of time.
 4. Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.
-

C

Population genetics is the study of:

1. how selective forces change the allele frequencies in a population over time
 2. the genetic basis of population-wide traits
 3. whether traits have a genetic basis
 4. the degree of inbreeding in a population
-

A

Which of the following populations is not in Hardy-Weinberg equilibrium?

1. a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy)

2. a population in which the allele frequencies do not change over time
 3. $p^2 + 2pq + q^2 = 1$
 4. a population undergoing natural selection
-

D

One of the original Amish colonies rose from a ship of colonists that came from Europe. The ship's captain, who had polydactyly, a rare dominant trait, was one of the original colonists. Today, we see a much higher frequency of polydactyly in the Amish population. This is an example of:

1. natural selection
 2. genetic drift
 3. founder effect
 4. b and c
-

D

Free Response

Solve for the genetic structure of a population

with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy).

$$p = (8 \cdot 2 + 4) / 48 = .42; q = (12 \cdot 2 + 4) / 48 = .58; p^2 = .17; 2pq = .48; q^2 = .34$$

Explain the Hardy-Weinberg principle of equilibrium theory.

The Hardy-Weinberg principle of equilibrium is used to describe the genetic makeup of a population. The theory states that a population's allele and genotype frequencies are inherently stable: unless some kind of evolutionary force is acting upon the population, generation after generation of the population would carry the same genes, and individuals would, as a whole, look essentially the same.

Imagine you are trying to test whether a population of flowers is undergoing evolution. You suspect there is selection pressure on the color of the flower: bees seem to cluster around the red flowers more often than the blue flowers. In a separate experiment, you discover blue flower color is dominant to red flower

color. In a field, you count 600 blue flowers and 200 red flowers. What would you expect the genetic structure of the flowers to be?

Red is recessive so $q^2 = 200/800 = 0.25$; $q = 0.5$; $p = 1 - q = 0.5$; $p^2 = 0.25$; $2pq = 0.5$. You would expect 200 homozygous blue flowers, 400 heterozygous blue flowers, and 200 red flowers.

Glossary

allele frequency

(also, gene frequency) rate at which a specific allele appears within a population

founder effect

event that initiates an allele frequency change in part of the population, which is not typical of the original population

gene pool

all of the alleles carried by all of the individuals in the population

genetic structure

distribution of the different possible genotypes in a population

macroevolution

broader scale evolutionary changes seen over paleontological time

microevolution

changes in a population's genetic structure

modern synthesis

overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

population genetics

study of how selective forces change the allele frequencies in a population over time

Population Genetics

By the end of this section, you will be able to:

- Describe the different types of variation in a population
- Explain why only heritable variation can be acted upon by natural selection
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence the allele frequencies of a population

Individuals of a population often display different phenotypes, or express different alleles of a particular gene, referred to as polymorphisms.

Populations with two or more variations of particular characteristics are called polymorphic.

The distribution of phenotypes among individuals, known as the **population variation**, is influenced by a number of factors, including the population's genetic structure and the environment ([\[link\]](#)).

Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.

The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)



Genetic Variance

Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected for, while deleterious alleles may be selected against. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a body builder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

Link to Learning



Before Darwinian evolution became the prevailing theory of the field, French naturalist Jean-Baptiste Lamarck theorized that acquired traits could, in fact, be inherited; while this hypothesis has largely been unsupported, scientists have recently begun to realize that Lamarck was not completely wrong. Visit this [site](#) to learn more.

Heritability is the fraction of phenotype variation that can be attributed to genetic differences, or genetic variance, among individuals in a population. The greater the heritability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

The diversity of alleles and genotypes within a population is called **genetic variance**. When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves,

they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with **inbreeding**, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease. For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as **inbreeding depression**.

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and

environmental variances.

A chance event or catastrophe can reduce the genetic variability within a population. A. J. Tipping et al., “Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa,” *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population’s silverback, the pack’s leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular **selection pressure**, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is **genetic drift** ([\[link\]](#)), which is simply the effect of chance. By chance, some individuals will have more offspring than others—not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

Art Connection

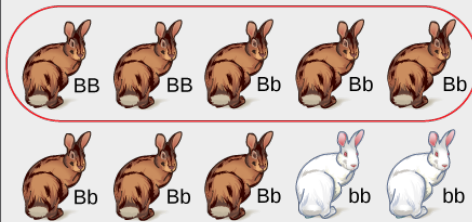
Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (B) are dominant over rabbits with the white coat color allele (b). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of .5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive b allele is lost.

Genetic Drift

First generation

p (B gene frequency) = .5

q (b gene frequency) = .5



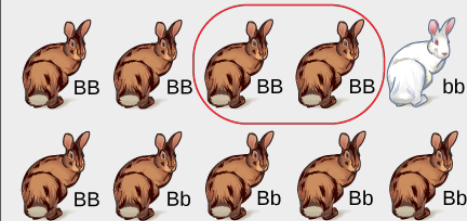
5 rabbits reproduce



Second generation

p = .7

q = .3



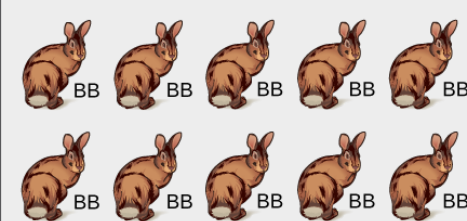
2 rabbits reproduce



Third generation

p = 1

q = 0



Do you think genetic drift would happen more quickly on an island or on the mainland?

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

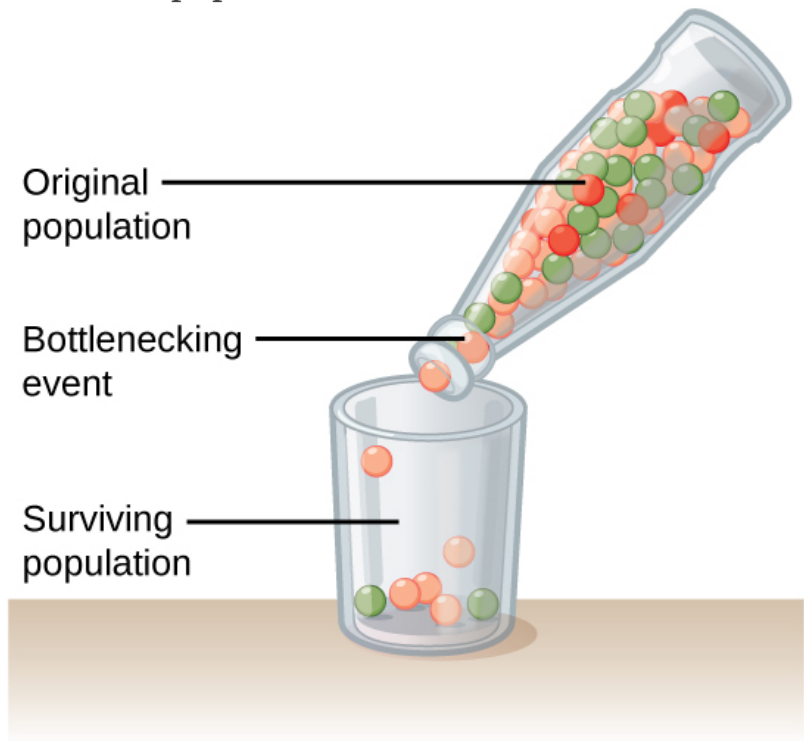
Link to Learning



Go to this [site](#) to watch an animation of random sampling and genetic drift in action.

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known

as the **bottleneck effect**, it results in a large portion of the genome suddenly being wiped out ([\[link\]](#)). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.



Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population, which results in the founder effect. The founder effect

occurs when the genetic structure changes to match that of the new population's founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.[\[footnote\]](#)

Link to Learning



Watch this short video to learn more about the founder and bottleneck effects.

https://www.openstaxcollege.org/l/founder_bottle

Scientific Method Connection

Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out the original population using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour $\frac{1}{3}$ of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the

populations all contain the same number of different colored beads, or do they vary? Remember, these populations all came from the same exact parent population.

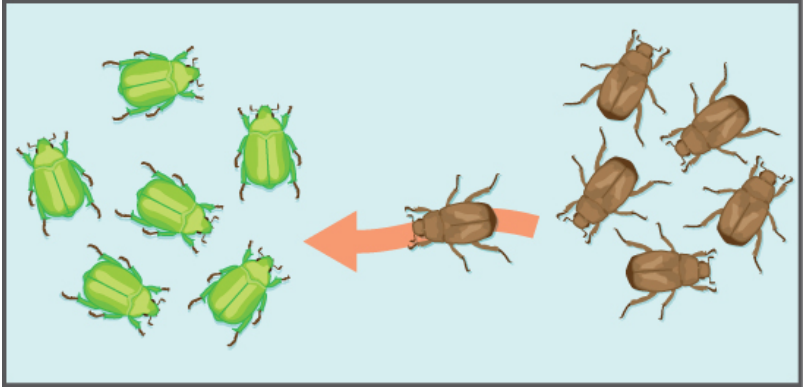
Form a conclusion: Most likely, the five resulting populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

Gene flow can occur when an individual travels from one geographic location to another.

Gene Flow

Another important evolutionary force is **gene flow**: the flow of alleles in and out of a population due to the migration of individuals or gametes ([\[link\]](#)). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers

to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but it can also introduce new genetic variation to populations in different geological locations and habitats.



Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and

reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome. Some can have a dramatic effect on a gene and the resulting phenotype.

Nonrandom Mating

If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons **nonrandom mating** occurs. One reason is simple mate choice; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual become selected for by natural selection. One common form of mate choice, called **assortative mating**, is an individual's preference to mate with partners who are phenotypically similar to themselves.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.

The sex of the American alligator (*Alligator mississippiensis*) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C

produce males. (credit: Steve Hillebrand, USFWS)

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment ([link](#)). A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as sex, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.



Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such **geographical variation** is seen between most populations and can be significant. One type of geographic variation, called a **cline**, can be seen as populations of a given species vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

Section Summary

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can be passed to its

offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the germ line have more offspring than others. When individuals leave or join the population, allele frequencies can change as a result of gene flow. Mutations to an individual's DNA may introduce new variation into a population. Allele frequencies can also be altered when individuals do not randomly mate with others in the group.

Art Connections

[\[link\]](#) Do you think genetic drift would happen more quickly on an island or on the mainland?

[\[link\]](#) Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

Review Questions

When male lions reach sexual maturity, they leave their group in search of a new pride. This can alter the allele frequencies of the population through which of the following mechanisms?

1. natural selection
 2. genetic drift
 3. gene flow
 4. random mating
-

C

Which of the following evolutionary forces can introduce new genetic variation into a population?

1. natural selection and genetic drift
 2. mutation and gene flow
 3. natural selection and nonrandom mating
 4. mutation and genetic drift
-

B

What is assortative mating?

1. when individuals mate with those who are similar to themselves

2. when individuals mate with those who are dissimilar to themselves
 3. when individuals mate with those who are the most fit in the population
 4. when individuals mate with those who are least fit in the population
-

A

When closely related individuals mate with each other, or inbreed, the offspring are often not as fit as the offspring of two unrelated individuals. Why?

1. Close relatives are genetically incompatible.
 2. The DNA of close relatives reacts negatively in the offspring.
 3. Inbreeding can bring together rare, deleterious mutations that lead to harmful phenotypes.
 4. Inbreeding causes normally silent alleles to be expressed.
-

C

What is a cline?

1. the slope of a mountain where a population lives
 2. the degree to which a mutation helps an individual survive
 3. the number of individuals in the population
 4. gradual geographic variation across an ecological gradient
-

D

Free Response

Describe a situation in which a population would undergo the bottleneck effect and explain what impact that would have on the population's gene pool.

A hurricane kills a large percentage of a population of sand-dwelling crustaceans—only a few individuals survive. The alleles carried by those surviving individuals would represent the entire population's gene pool. If those surviving individuals are not representative of the original population, the post-hurricane gene pool will differ from the original gene pool.

Describe natural selection and give an example of natural selection at work in a population.

The theory of natural selection stems from the observation that some individuals in a population survive longer and have more offspring than others: thus, more of their genes are passed to the next generation. For example, a big, powerful male gorilla is much more likely than a smaller, weaker one to become the population's silverback: the pack's leader who mates far more than the other males of the group. Therefore, the pack leader will father more offspring who share half of his genes and are likely to grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the average body size, as a result, grow larger on average.

Explain what a cline is and provide examples.

A cline is a type of geographic variation that is seen in populations of a given species that vary gradually across an ecological gradient. For example, warm-blooded animals tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline.

Flowering plants tend to bloom at different times depending on where they are along the slope of a mountain. This is known as an altitudinal cline.

Glossary

assortative mating

when individuals tend to mate with those who are phenotypically similar to themselves

bottleneck effect

magnification of genetic drift as a result of natural events or catastrophes

cline

gradual geographic variation across an ecological gradient

gene flow

flow of alleles in and out of a population due to the migration of individuals or gametes

genetic drift

effect of chance on a population's gene pool

genetic variance

diversity of alleles and genotypes in a population

geographical variation

differences in the phenotypic variation
between populations that are separated
geographically

heritability

fraction of population variation that can be
attributed to its genetic variance

inbreeding

mating of closely related individuals

inbreeding depression

increase in abnormalities and disease in
inbreeding populations

nonrandom mating

changes in a population's gene pool due to
mate choice or other forces that cause
individuals to mate with certain phenotypes
more than others

population variation

distribution of phenotypes in a population

selective pressure

environmental factor that causes one
phenotype to be better than another

Formation of New Species

By the end of this section, you will be able to:

- Define species and describe how species are identified as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation

Although all life on earth shares various genetic similarities, only certain organisms combine genetic information by sexual reproduction and have offspring that can then successfully reproduce. Scientists call such organisms members of the same biological species.

The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo.

(credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)

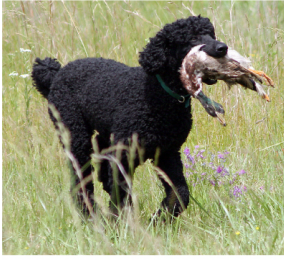
The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species. (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service)

Species and the Ability to Reproduce

A **species** is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

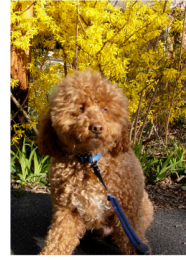
Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce ([link](#)).



(a)



(b)



(c)

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group ([\[link\]](#)). If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a **hybrid** (a cross between two species), would probably be infertile—unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.



(a)



(b)

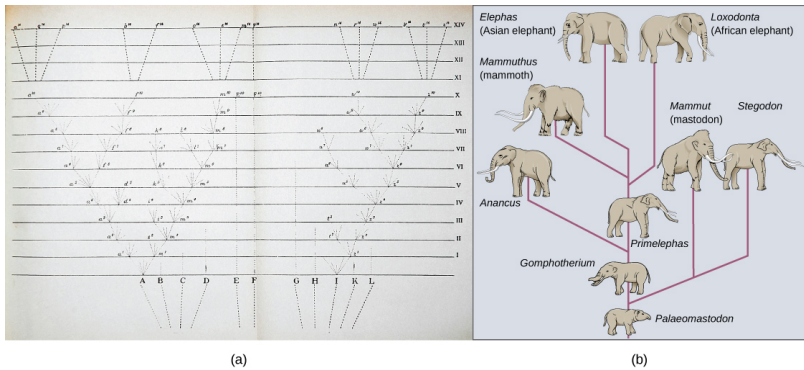
Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

The only illustration in Darwin's *On the Origin of Species* is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the *Palaeomastodon*, a species that lived in Egypt 35–50 million years ago.

Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* ([\[link\]](#)**a**). Compare this illustration to the diagram of elephant evolution ([\[link\]](#)**b**), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.



For speciation to occur, two new populations must be formed from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and multiple events can be conceptualized as single splits occurring close in time.

The northern spotted owl and the Mexican spotted

owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke) The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Allopatric Speciation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural

selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. **Dispersal** is when a few members of a species move to a new geographical area, and **vicariance** is when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic

differences from its close relative: the Mexican spotted owl, which lives in the south ([link](#)).

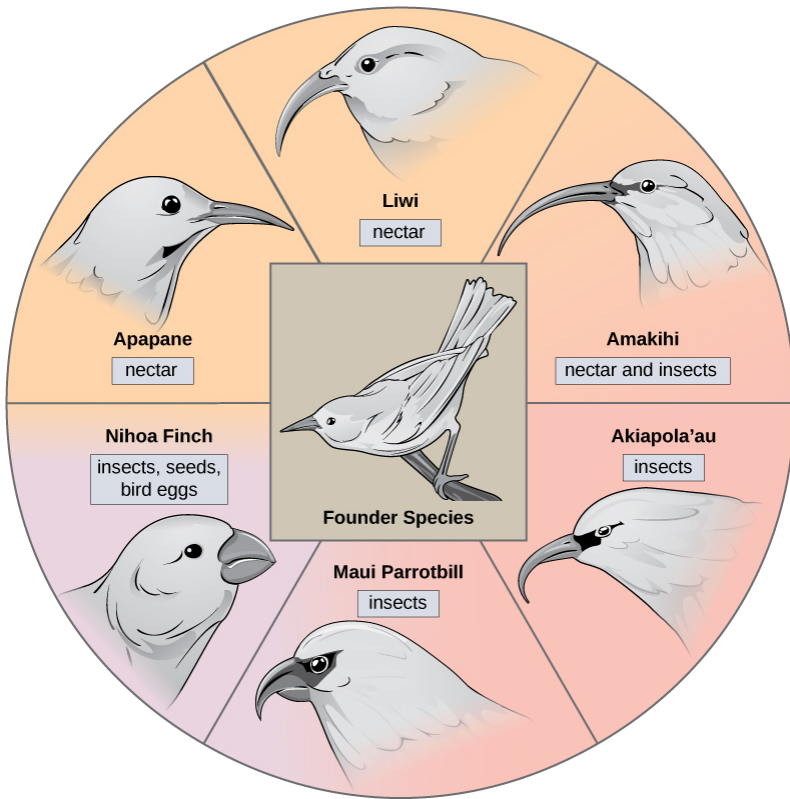


Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south; the types of organisms in each ecosystem differ, as

do their behaviors and habits; also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called **adaptive radiation** because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the six shown in [\[link\]](#).



Notice the differences in the species' beaks in [\[link\]](#). Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

Link to Learning



Click through this [interactive site](#) to see how island birds evolved in evolutionary increments from 5 million years ago to today.

Autopolyploidy results when mitosis is not followed by cytokinesis. Allopolyploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

Sympatric Speciation

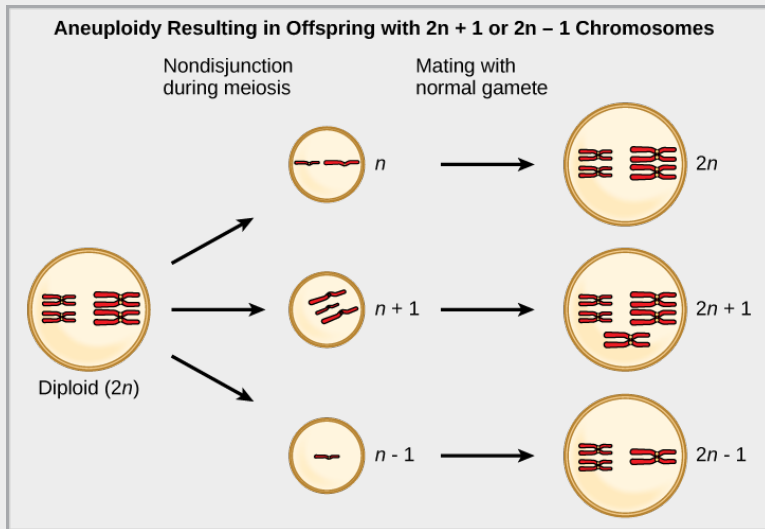
Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called sympatric speciation; the prefix “sym” means same, so “sympatric” means “same homeland” in contrast to “allopatric” meaning

“other homeland.” A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called **aneuploidy** ([\[link\]](#)).

Art Connection

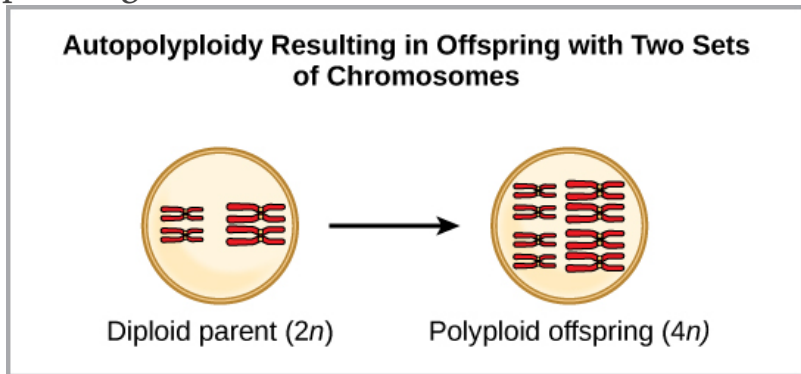
Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have $2n + 1$ or $2n - 1$ chromosomes



Which is most likely to survive, offspring with $2n + 1$ chromosomes or offspring with $2n - 1$ chromosomes?

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called **autopolyploidy** ([\[link\]](#)). The prefix “auto-” means “self,” so the term means multiple chromosomes from one’s own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of

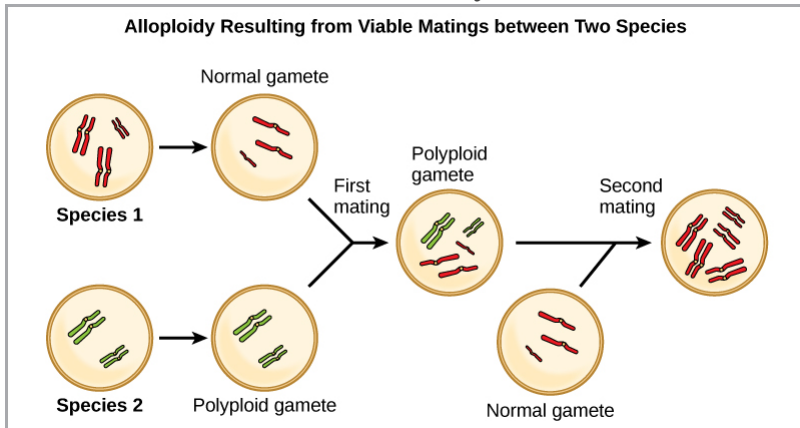
separating.



For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an **allopolyploid**. The prefix “allo-” means “other” (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. [\[link\]](#) illustrates

one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.



The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

These two related frog species exhibit temporal reproductive isolation. (a) *Rana aurora* breeds earlier in the year than (b) *Rana boylei*. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi) Speciation can occur when two

populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated. The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species.

Reproductive organ incompatibility keeps the species reproductively isolated. Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds. Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together,

mating would be less likely, but if mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the **reproductive isolation**, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a **prezygotic barrier** is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A **postzygotic barrier** occurs after zygote formation; this includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called **temporal isolation**, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May ([link](#)).

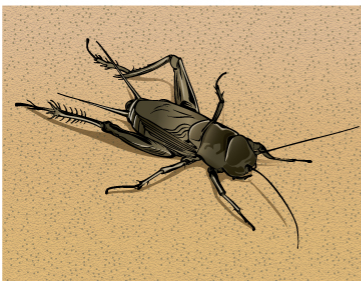


(a)

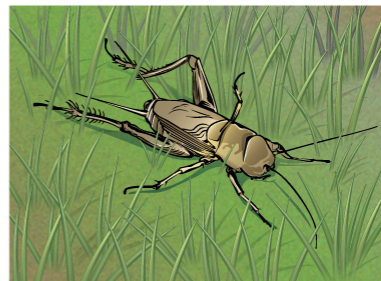


(b)

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the other populations of the same species. This situation is called **habitat isolation**. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups ([link](#)).



(a) *Gryllus pennsylvanicus* prefers sandy soil.

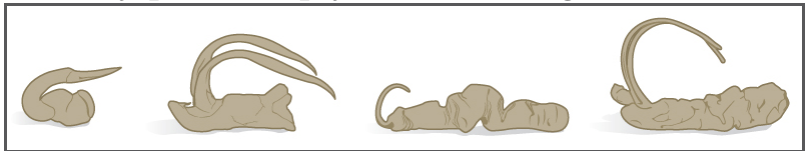


(b) *Gryllus firmus* prefers loamy soil.

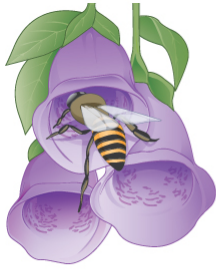
Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction

from taking place. For example, male fireflies use specific light patterns to attract females. Various species of fireflies display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place; this is called a **gametic barrier**. Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. ([link](#)).



In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from being cross-pollinated with a different species ([link](#)).



(a) Honeybee drinking nectar from a foxglove flower



(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

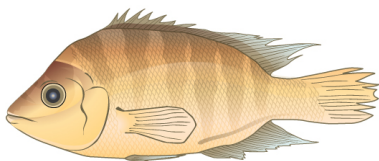
When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. This is called **hybrid inviability** because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Habitat Influence on Speciation

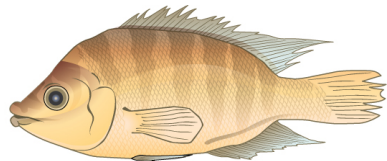
Sympatric speciation may also take place in ways other than polyploidy. For example, consider a species of fish that lives in a lake. As the population grows, competition for food also grows. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with

each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. [\[link\]](#) shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.



Thin-lipped cichlid



Thick-lipped cichlid

Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and

through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways isolate a population reproductively in some form. Mechanisms of reproductive isolation act as barriers between closely related species, enabling them to diverge and exist as genetically independent species. Prezygotic barriers block reproduction prior to formation of a zygote, whereas postzygotic barriers block reproduction after fertilization occurs. For a new species to develop, something must cause a breach in the reproductive barriers. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes (polyploidy). Autopolyploidy occurs within a single species, whereas allopolyploidy occurs between closely related species.

Art Connections

[\[link\]](#) Which is most likely to survive, offspring with $2n + 1$ chromosomes or offspring with $2n - 1$ chromosomes?

[\[link\]](#) Loss of genetic material is almost always lethal, so offspring with $2n + 1$ chromosomes are more likely to survive.

Review Questions

Which situation would most likely lead to allopatric speciation?

1. flood causes the formation of a new lake.
2. A storm causes several large trees to fall down.
3. A mutation causes a new trait to develop.
4. An injury causes an organism to seek out a new food source.

A

What is the main difference between dispersal and vicariance?

1. One leads to allopatric speciation, whereas the other leads to sympatric speciation.
 2. One involves the movement of the organism, and the other involves a change in the environment.
 3. One depends on a genetic mutation occurring, and the other does not.
 4. One involves closely related organisms, and the other involves only individuals of the same species.
-

B

Which variable increases the likelihood of allopatric speciation taking place more quickly?

1. lower rate of mutation
2. longer distance between divided groups
3. increased instances of hybrid formation
4. equivalent numbers of individuals in each population

B

What is the main difference between autopolyploid and allopolyploid?

1. the number of chromosomes
2. the functionality of the chromosomes
3. the source of the extra chromosomes
4. the number of mutations in the extra chromosomes

C

Which reproductive combination produces hybrids?

1. when individuals of the same species in different geographical areas reproduce
 2. when any two individuals sharing the same habitat reproduce
 3. when members of closely related species reproduce
 4. when offspring of the same parents reproduce
-

C

Which condition is the basis for a species to be reproductively isolated from other members?

1. It does not share its habitat with related species.
 2. It does not exist out of a single habitat.
 3. It does not exchange genetic information with other species.
 4. It does not undergo evolutionary changes for a significant period of time.
-

C

Which situation is *not* an example of a prezygotic barrier?

1. Two species of turtles breed at different

- times of the year.
2. Two species of flowers attract different pollinators.
 3. Two species of birds display different mating dances.
 4. Two species of insects produce infertile offspring.
-

D

Free Response

Why do island chains provide ideal conditions for adaptive radiation to occur?

Organisms of one species can arrive to an island together and then disperse throughout the chain, each settling into different niches and exploiting different food resources to reduce competition.

Two species of fish had recently undergone sympatric speciation. The males of each species had a different coloring through which the females could identify and choose a partner

from her own species. After some time, pollution made the lake so cloudy that it was hard for females to distinguish colors. What might take place in this situation?

It is likely the two species would start to reproduce with each other. Depending on the viability of their offspring, they may fuse back into one species.

Why can polyploidy individuals lead to speciation fairly quickly?

The formation of gametes with new n numbers can occur in one generation. After a couple of generations, enough of these new hybrids can form to reproduce together as a new species.

Glossary

adaptive radiation

speciation when one species radiates out to form several other species

allopatric speciation

speciation that occurs via geographic separation

allopolyploid

polyploidy formed between two related, but separate species

aneuploidy

condition of a cell having an extra chromosome or missing a chromosome for its species

autopolyploid

polyploidy formed within a single species

behavioral isolation

type of reproductive isolation that occurs when a specific behavior or lack of one prevents reproduction from taking place

dispersal

allopatric speciation that occurs when a few members of a species move to a new geographical area

gametic barrier

prezygotic barrier occurring when closely related individuals of different species mate, but differences in their gamete cells (eggs and sperm) prevent fertilization from taking place

habitat isolation

reproductive isolation resulting when populations of a species move or are moved to a new habitat, taking up residence in a

place that no longer overlaps with the other populations of the same species

hybrid

offspring of two closely related individuals, not of the same species

postzygotic barrier

reproductive isolation mechanism that occurs after zygote formation

prezygotic barrier

reproductive isolation mechanism that occurs before zygote formation

reproductive isolation

situation that occurs when a species is reproductively independent from other species; this may be brought about by behavior, location, or reproductive barriers

speciation

formation of a new species

species

group of populations that interbreed and produce fertile offspring

sympatric speciation

speciation that occurs in the same geographic space

temporal isolation

differences in breeding schedules that can act as a form of prezygotic barrier leading to reproductive isolation

vicariance

allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

Organizing Life on Earth

By the end of this section, you will be able to:

- Discuss the need for a comprehensive classification system
- List the different levels of the taxonomic classification system
- Describe how systematics and taxonomy relate to phylogeny
- Discuss the components and purpose of a phylogenetic tree

In scientific terms, the evolutionary history and relationship of an organism or group of organisms is called its **phylogeny**. A phylogeny describes the relationships of an organism, such as from which organisms it is thought to have evolved, to which species it is most closely related, and so forth. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba) The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and

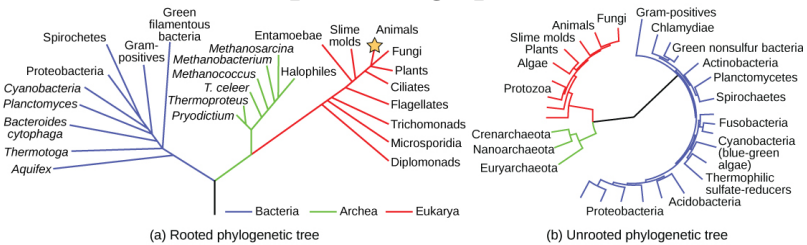
remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

Phylogenetic Trees

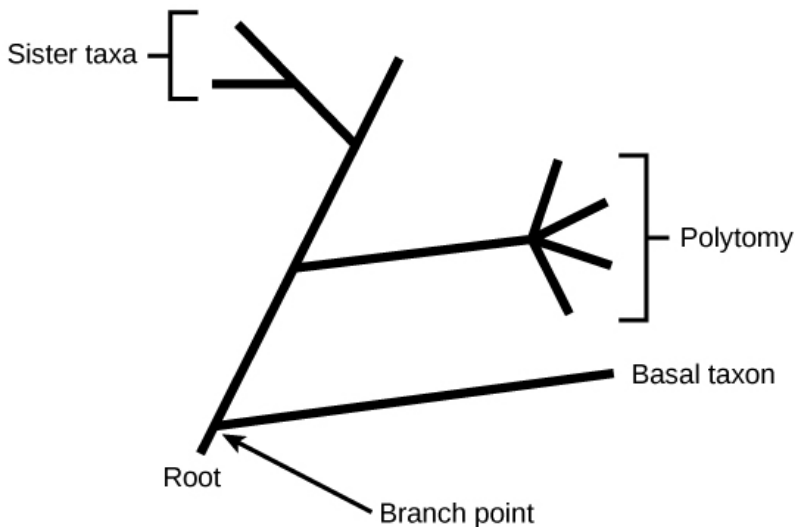
Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms ([\[link\]](#)).

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees **rooted**, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains—Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy

in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don't show a common ancestor but do show relationships among species.



In a rooted tree, the branching indicates evolutionary relationships ([\[link\]](#)). The point where a split occurs, called a **branch point**, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called **basal taxon**. When two lineages stem from the same branch point, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.



The diagrams above can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover that species' ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

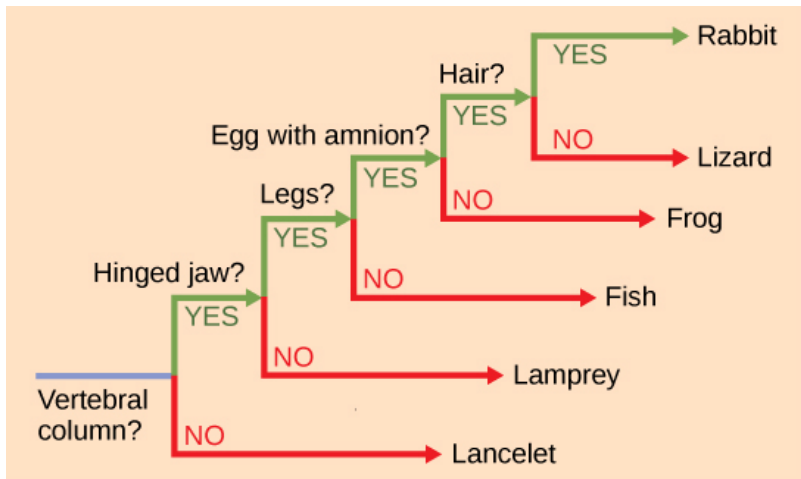
Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called **systematics**. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

Limitations of Phylogenetic Trees

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic

tree in [\[link\]](#) shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.



Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in [\[link\]](#), the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using [\[link\]](#), the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in

[link], just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.

Link to Learning



Head to this [website](#) to see interactive exercises that allow you to explore the evolutionary relationships among species.

The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo. (credit “dog”: modification of work by Janneke Vreugdenhil)

The Levels of Classification

Taxonomy (which literally means “arrangement law”) is the science of classifying organisms to construct internationally shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then finally a single product. This organization from larger to smaller, more specific categories is called a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are: **phylum**, **class**, **order**, **family**, **genus**, and **species** ([\[link\]](#)).



Subspecies: *Canus lupus familiaris*

Species: *Canis lupus*

Genus: *Canis*

Family: Canidae

Order: Carnivora

Class: Mammalia

Phylum: Chordata

Kingdom: Animalia

Domain: Eukarya

The kingdom Animalia stems from the Eukarya














































domain. For the common dog, the classification levels would be as shown in [\[link\]](#). Therefore, the full name of an organism technically has eight terms. For the dog, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called **binomial nomenclature**. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a **taxon**. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the “*familiaris*” in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

[\[link\]](#) shows how the levels move toward specificity with other organisms. Notice how the dog shares a domain with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists classified organisms using characteristics, but as

DNA technology developed, more precise phylogenies have been determined.

Art Connection

At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by "berduchwal"/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf”: modification of work by Robert Dewar; credit “dog”: modification of work by "digital_image_fan"/Flickr)

Subspecies: <i>Canis lupus familiaris</i>	 Dog
Species: <i>Canis lupus</i>	  Wolf Dog
Genus: <i>Canis</i>	   Jackal Wolf Dog
Family: Canidae	    Fox Jackal Wolf Dog
Order: Carnivora	     Cat Fox Jackal Wolf Dog
Class: Mammalia	      Rabbit Cat Fox Jackal Wolf Dog
Phylum: Chordata	       Fish Rabbit Cat Fox Jackal Wolf Dog
Kingdom: Animalia	        Insect Fish Rabbit Cat Fox Jackal Wolf Dog
Domain: Eukarya	         Plant Insect Fish Rabbit Cat Fox Jackal Wolf Dog

At what levels are cats and dogs considered to be part of the same group?

Link to Learning



Visit this [website](#) to classify three organisms—bear, orchid, and sea cucumber—from kingdom to species. To launch the game, under Classifying Life, click the picture of the bear or the Launch Interactive button.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative of the whale.

Section Summary

Scientists continually gain new information that helps understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny.

Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

Art Connections

[\[link\]](#) At what levels are cats and dogs considered to be part of the same group?

[\[link\]](#) Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Review Questions

What is used to determine phylogeny?

1. mutations
2. DNA

3. evolutionary history
 4. organisms on earth
-

C

What do scientists in the field of systematics accomplish?

1. discover new fossil sites
 2. organize and classify organisms
 3. name new species
 4. communicate among field biologists
-

B

Which statement about the taxonomic classification system is correct?

1. There are more domains than kingdoms.
 2. Kingdoms are the top category of classification.
 3. Classes are divisions of orders.
 4. Subspecies are the most specific category of classification.
-

D

On a phylogenetic tree, which term refers to lineages that diverged from the same place?

1. sister taxa
2. basal taxa
3. rooted taxa
4. dichotomous taxa

A

Free Response

How does a phylogenetic tree relate to the passing of time?

The phylogenetic tree shows the order in which evolutionary events took place and in what order certain characteristics and organisms evolved in relation to others. It does not relate to time.

Some organisms that appear very closely related on a phylogenetic tree may not actually be closely related. Why is this?

In most cases, organisms that appear closely related actually are; however, there are cases where organisms evolved through convergence and appear closely related but are not.

List the different levels of the taxonomic classification system.

domain, kingdom, phylum, class, order, family, genus, species

Glossary

basal taxon

branch on a phylogenetic tree that has not diverged significantly from the root ancestor

binomial nomenclature

system of two-part scientific names for an organism, which includes genus and species names

branch point

node on a phylogenetic tree where a single lineage splits into distinct new ones

class

division of phylum in the taxonomic classification system

family

division of order in the taxonomic classification system

genus

division of family in the taxonomic classification system; the first part of the binomial scientific name

kingdom

division of domain in the taxonomic classification system

order

division of class in the taxonomic classification system

phylogenetic tree

diagram used to reflect the evolutionary relationships among organisms or groups of organisms

phylogeny

evolutionary history and relationship of an organism or group of organisms

phylum

(plural: phyla) division of kingdom in the taxonomic classification system

polytomy

branch on a phylogenetic tree with more than

two groups or taxa

rooted

single ancestral lineage on a phylogenetic tree to which all organisms represented in the diagram relate

sister taxa

two lineages that diverged from the same branch point

systematics

field of organizing and classifying organisms based on evolutionary relationships

taxon

(plural: taxa) single level in the taxonomic classification system

taxonomy

science of classifying organisms

Characteristics of Protists

By the end of this section, you will be able to:

- Describe the cell structure characteristics of protists
- Describe the metabolic diversity of protists
- Describe the life cycle diversity of protists

There are over 100,000 described living species of protists, and it is unclear how many undescribed species may exist. Since many protists live as commensals or parasites in other organisms and these relationships are often species-specific, there is a huge potential for protist diversity that matches the diversity of hosts. As the catchall term for eukaryotic organisms that are not animal, plant, or fungi, it is not surprising that very few characteristics are common to all protists.

Cell Structure

The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime, or in

other cases, like ferns. In fact, many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to three meters in length to hectares. Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with **pellicles** of interlocking protein strips. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

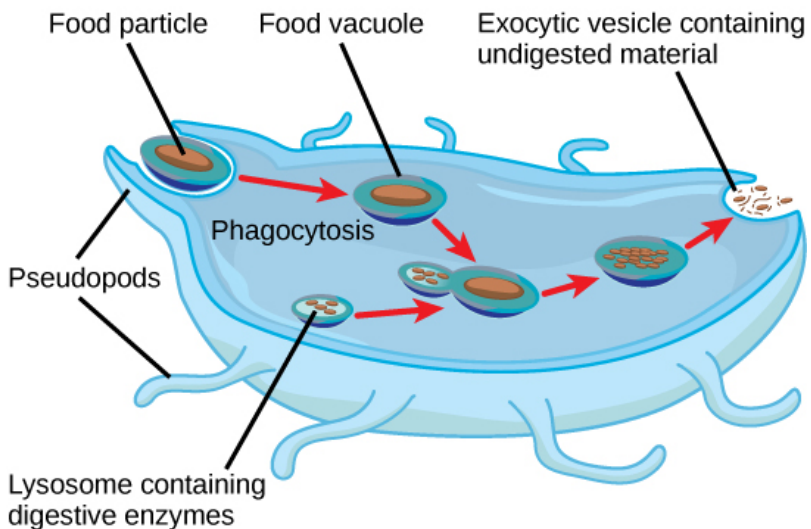
The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

Metabolism

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Protists that store energy by photosynthesis belong to a group of photoautotrophs and are characterized by the presence of chloroplasts. Other protists are heterotrophic and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called phagocytosis, in which

the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole ([link]). The vesicle containing the ingested particle, the phagosome, then fuses with a lysosome containing hydrolytic enzymes to produce a **phagolysosome**, and the food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell via exocytosis.

Phagocytosis

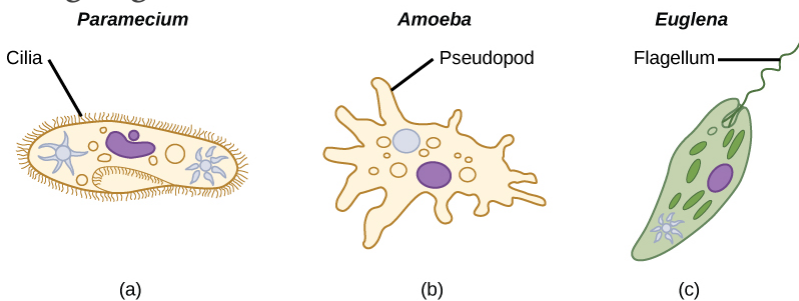


Subtypes of heterotrophs, called saprobes, absorb nutrients from dead organisms or their organic wastes. Some protists can function as **mixotrophs**, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available. Protists use various methods for transportation. (a)

Paramecium waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement ([\[link\]](#)). Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they coordinately beat to swim. Still others form cytoplasmic extensions called pseudopodia anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward. Some protists can move toward or away from a stimulus, a movement referred to as taxis. Movement toward light, termed phototaxis, is accomplished by coupling their locomotion strategy with a light-sensing organ.



Life Cycles

Protists reproduce by a variety of mechanisms. Most undergo some form of asexual reproduction, such as binary fission, to produce two daughter cells. In protists, binary fission can be divided into transverse or longitudinal, depending on the axis of orientation; sometimes *Paramecium* exhibits this method. Some protists such as the true slime molds exhibit multiple fission and simultaneously divide into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist. Sexual reproduction, involving meiosis and fertilization, is common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny that may be better suited to surviving in the new environment. However, sexual reproduction is often associated with resistant cysts that are a protective, resting stage. Depending on their habitat, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy also allows certain protists to “wait out” stressors until their environment becomes more favorable for survival or until they are carried (such as by wind, water, or transport on a larger organism) to a different environment, because cysts

exhibit virtually no cellular metabolism.

Protist life cycles range from simple to extremely elaborate. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, a strategy employed by animals. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Habitats

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Several protist species are parasites that infect animals or plants. A few protist species live on dead organisms or their wastes, and contribute to their decay.

Section Summary

Protists are extremely diverse in terms of their biological and ecological characteristics, partly because they are an artificial assemblage of

phylogenetically unrelated groups. Protists display highly varied cell structures, several types of reproductive strategies, virtually every possible type of nutrition, and varied habitats. Most single-celled protists are motile, but these organisms use diverse structures for transportation.

Review Questions

Protists that have a pellicle are surrounded by _____.

1. silica dioxide
2. calcium carbonate
3. carbohydrates
4. proteins

D

Protists with the capabilities to perform photosynthesis and to absorb nutrients from dead organisms are called _____.

1. photoautotrophs
2. mixotrophs
3. saprobes
4. heterotrophs

B

Which of these locomotor organs would likely be the shortest?

1. a flagellum
2. a cilium
3. an extended pseudopod
4. a pellicle

B

Alternation of generations describes which of the following?

1. The haploid form can be multicellular; the diploid form is unicellular.
2. The haploid form is unicellular; the diploid form can be multicellular.
3. Both the haploid and diploid forms can be multicellular.
4. Neither the haploid nor the diploid forms can be multicellular.

C

Free Response

Explain in your own words why sexual reproduction can be useful if a protist's environment changes.

The ability to perform sexual reproduction allows protists to recombine their genes and produce new variations of progeny that may be better suited to the new environment. In contrast, asexual reproduction generates progeny that are clones of the parent.

Giardia lamblia is a cyst-forming protist parasite that causes diarrhea if ingested. Given this information, against what type(s) of environments might *G. lamblia* cysts be particularly resistant?

As an intestinal parasite, *Giardia* cysts would be exposed to low pH in the stomach acids of its host. To survive this environment and reach the intestine, the cysts would have to be resistant to acidic conditions.

Glossary

mixotroph

organism that can obtain nutrition by autotrophic or heterotrophic means, usually facultatively

pellicle

outer cell covering composed of interlocking protein strips that function like a flexible coat of armor, preventing cells from being torn or pierced without compromising their range of motion

phagolysosome

cellular body formed by the union of a phagosome containing the ingested particle with a lysosome that contains hydrolytic enzymes

Groups of Protists

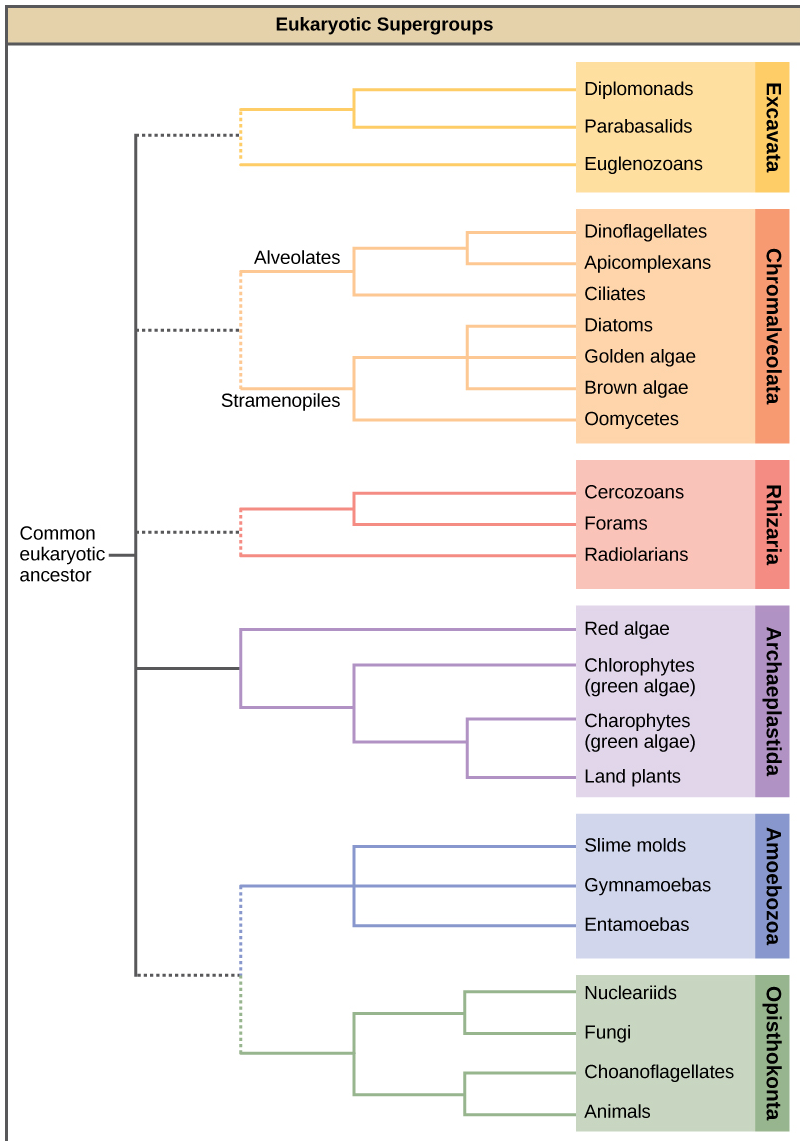
By the end of this section, you will be able to:

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called convergent evolution, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six “supergroups” that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor ([\[link\]](#)). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some

groups.

This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.



The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme

presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell) *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia*

([link](#)). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called **mitosomes**, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In

parabasalids, these structures function anaerobically and are called **hydrogenosomes** because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling.

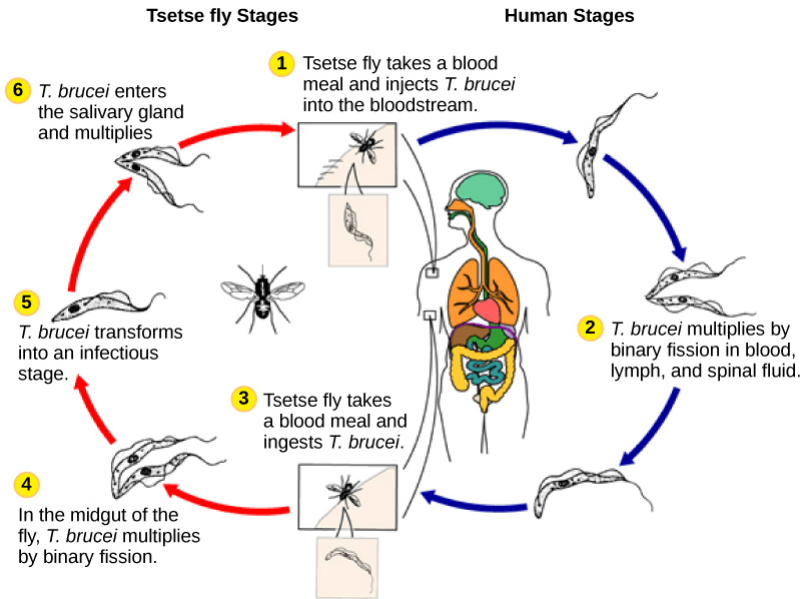
Trichomonas vaginalis, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichomoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 μm . Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their

environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the **kinetoplast**, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.



Link to Learning



Watch this video to see *T. brucei* swimming.
https://www.openstaxcollege.org/l/T_brucei

The dinoflagellates exhibit great diversity in shape.

Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion. Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: “catalano82”/Flickr) (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC) *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit “paramecium micrograph”: modification of work by NIH; scale-bar data from Matt Russell) This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum. Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 μm . (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA) A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Chromalveolata

Current evidence suggests that species classified as

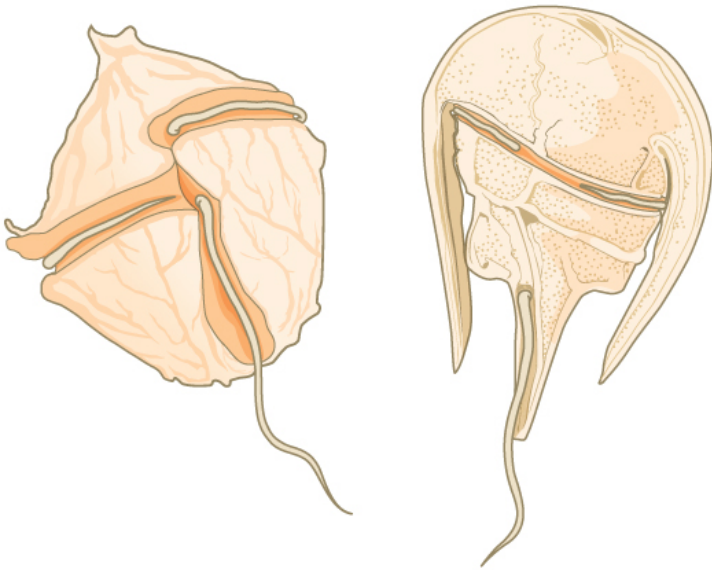
chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether. Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexans, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological

diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate ([\[link\]](#)). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of **plankton**, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.



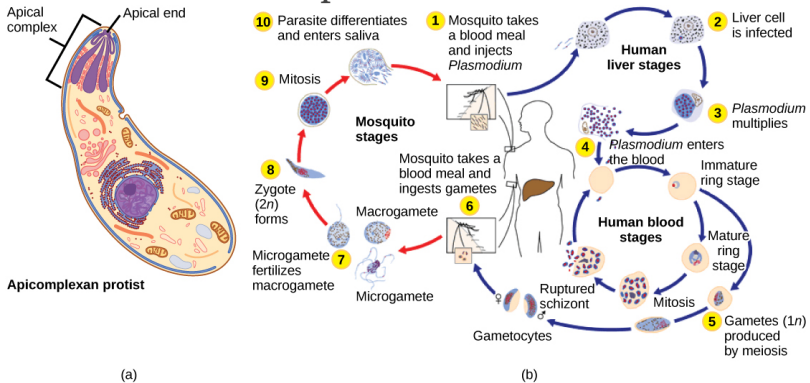
Some dinoflagellates generate light, called **bioluminescence**, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause

an entire breaking wave to twinkle or take on a brilliant blue color ([\[link\]](#)). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



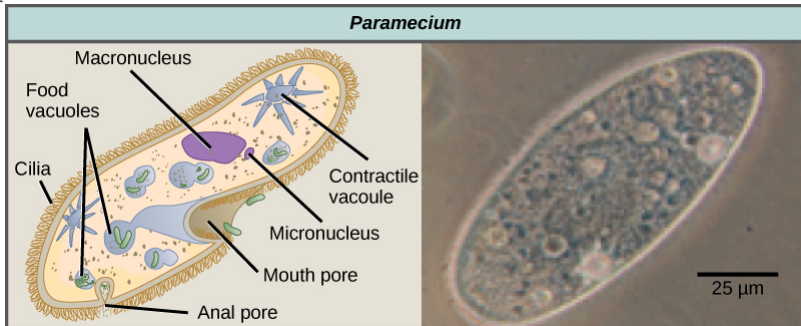
The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex ([\[link\]](#)). The apical complex is specialized for entry and infection

of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.



The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria ([link]). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on

the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses **contractile vacuoles**, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.



Link to Learning



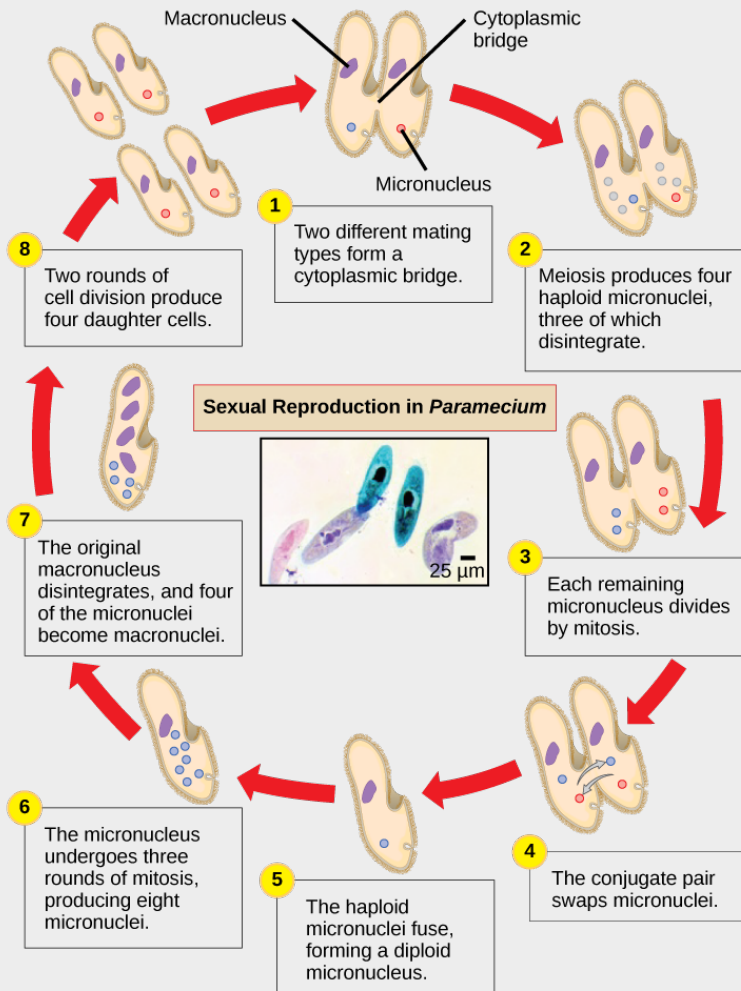
Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

<https://www.openstaxcollege.org/l/paramecium>

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge ([link]). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

Art Connection

The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit “micrograph”: modification of work by Ian Sutton; scale-bar data from Matt Russell)



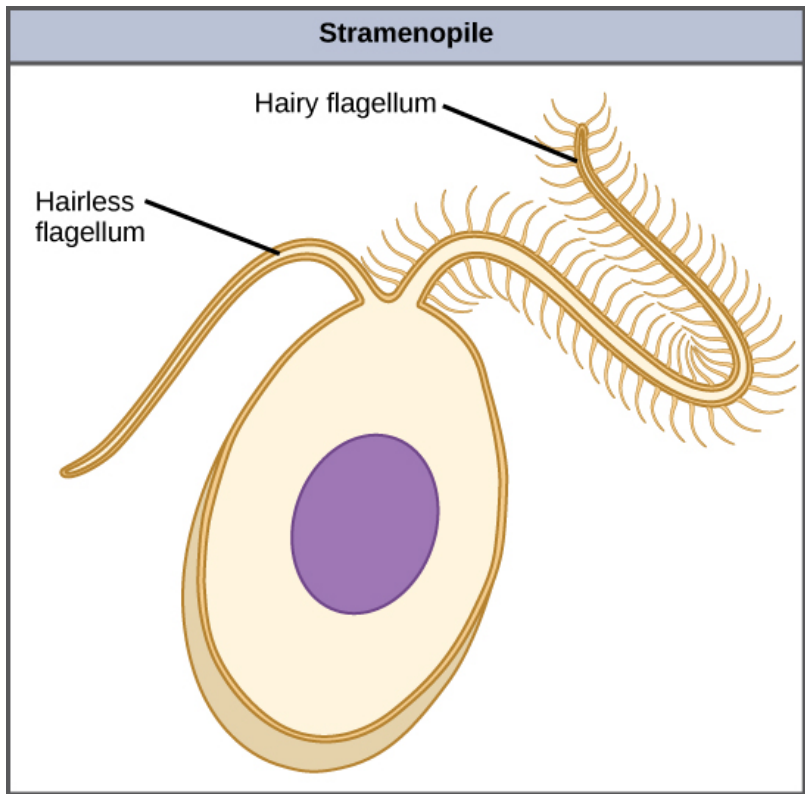
Which of the following statements about *Paramecium* sexual reproduction is false?

1. The macronuclei are derived from micronuclei.
2. Both mitosis and meiosis occur during sexual reproduction.
3. The conjugate pair swaps macronuclei.

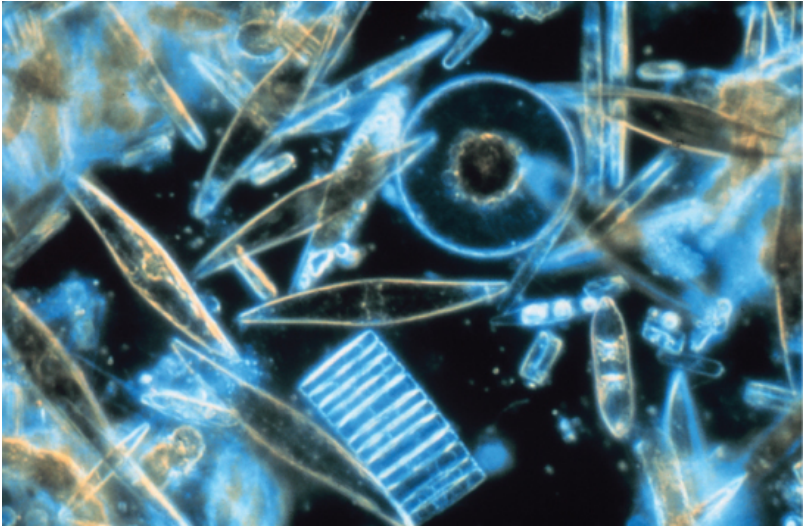
4. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or “hairy,” flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections ([\[link\]](#)). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.



The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles ([\[link\]](#)). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a **raphe**. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.



During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the **biological carbon pump**, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies.

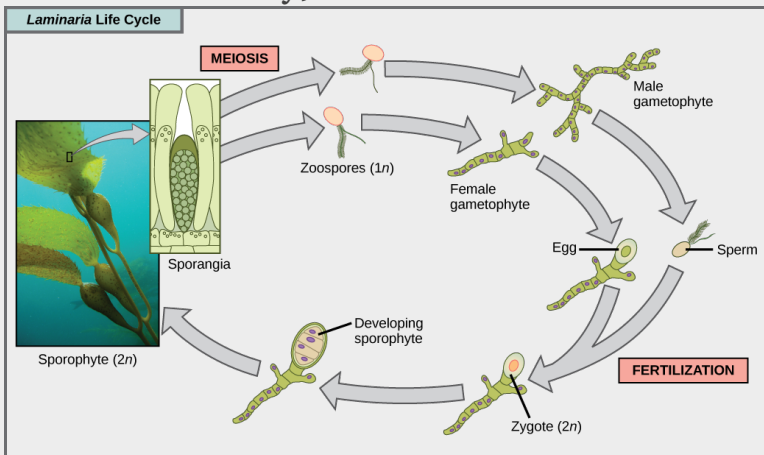
Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different

structure from the haploid form ([\[link\]](#)). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

Art Connection

Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit “laminaria photograph”: modification of work by Claire Fackler, CINMS, NOAA Photo Library)



Which of the following statements about the *Laminaria* life cycle is false?

1. $1n$ zoospores form in the sporangia.
2. The sporophyte is the $2n$ plant.

3. The gametophyte is diploid.
4. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes (“egg fungus”), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms ([\[link\]](#)). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.

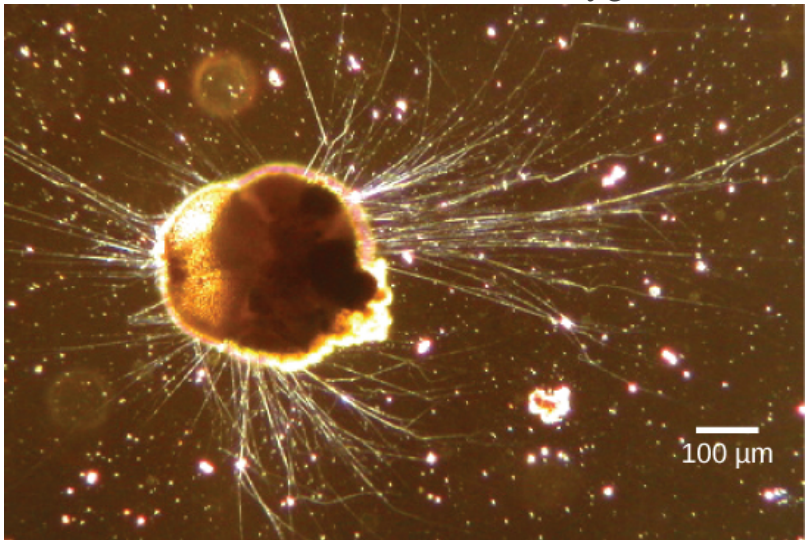


Ammonia tepida, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell) These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER) This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia ([\[link\]](#)). Pseudopodia function to

trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called **cytoplasmic streaming**, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.



Link to Learning

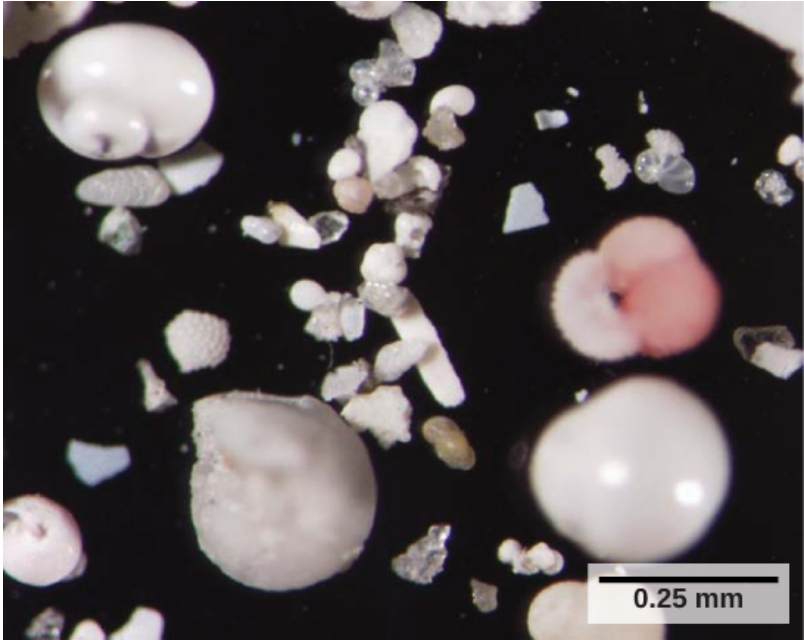


Take a look at this video to see cytoplasmic streaming in a green alga.

https://www.openstaxcollege.org/l/chara_corallina

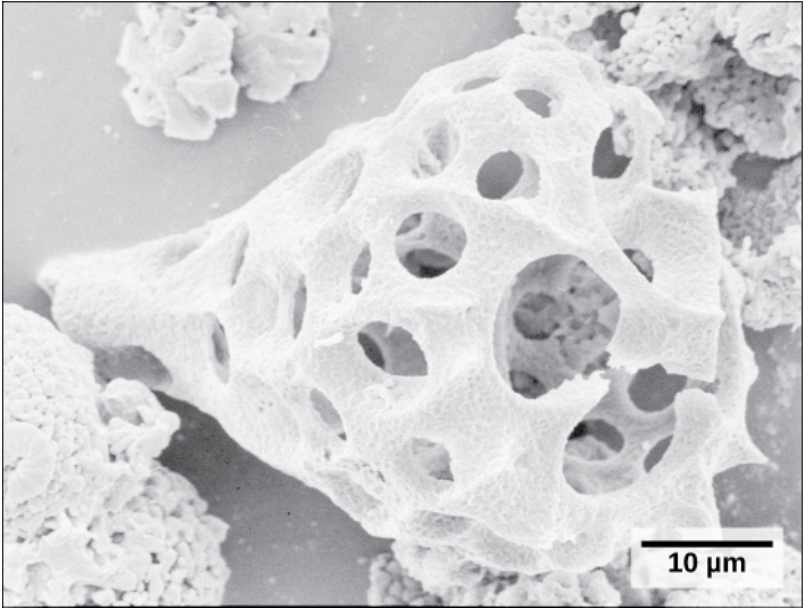
Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails ([link]). As a group, the forams exhibit porous shells, called **tests** that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Forams pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.



Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry ([\[link\]](#)). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.



Volvox aureus is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

Caulerpa taxifolia is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendants of an endosymbiotic

relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

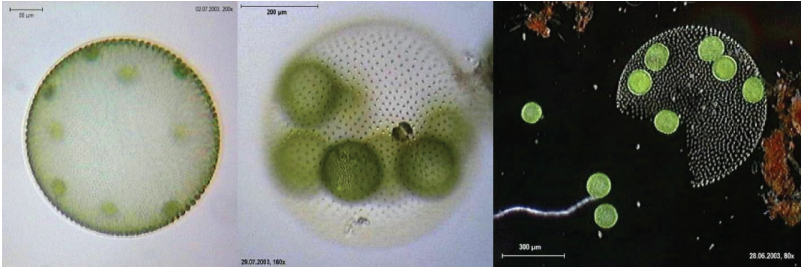
Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The

charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism ([\[link\]](#)). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters ([\[link\]](#)). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.

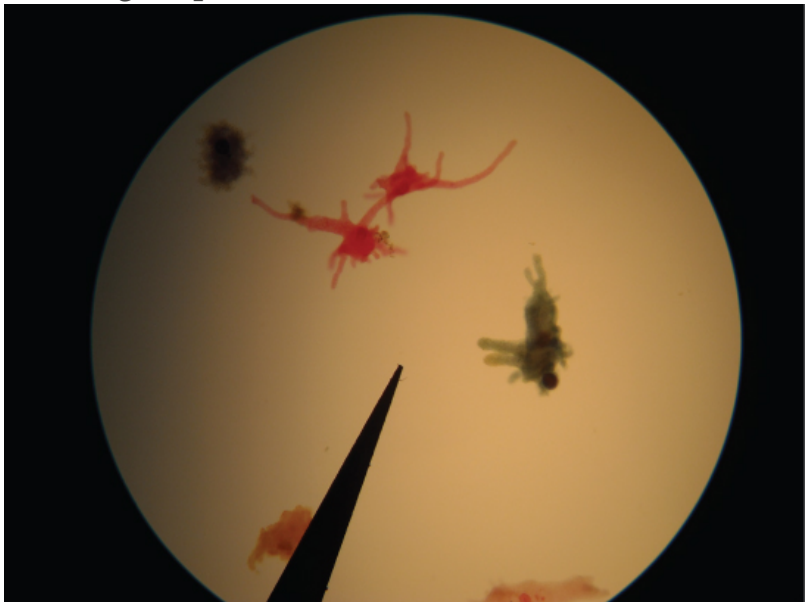


Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans. The life cycle of the plasmodial slime

mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University) Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by “thatredhead4”/ Flickr)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba ([\[link\]](#)). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

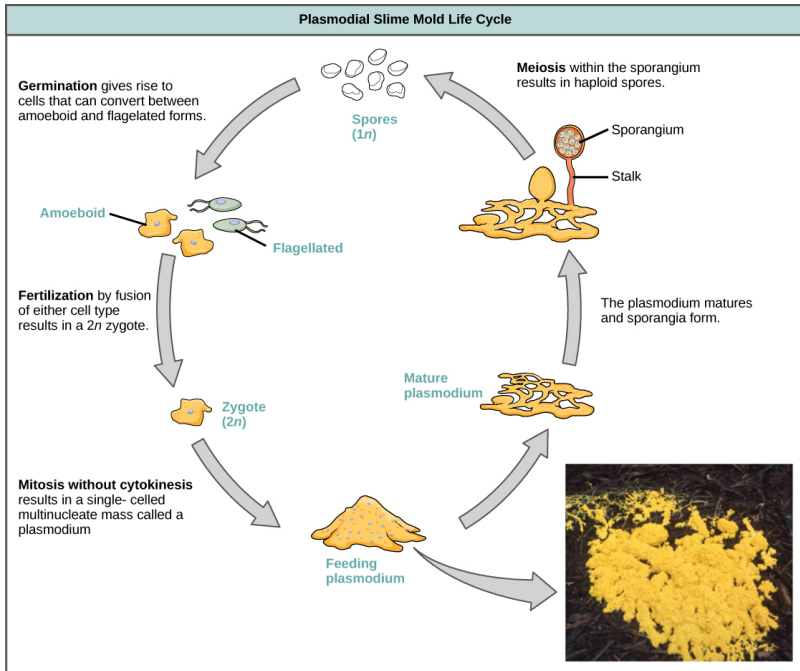


Slime Molds

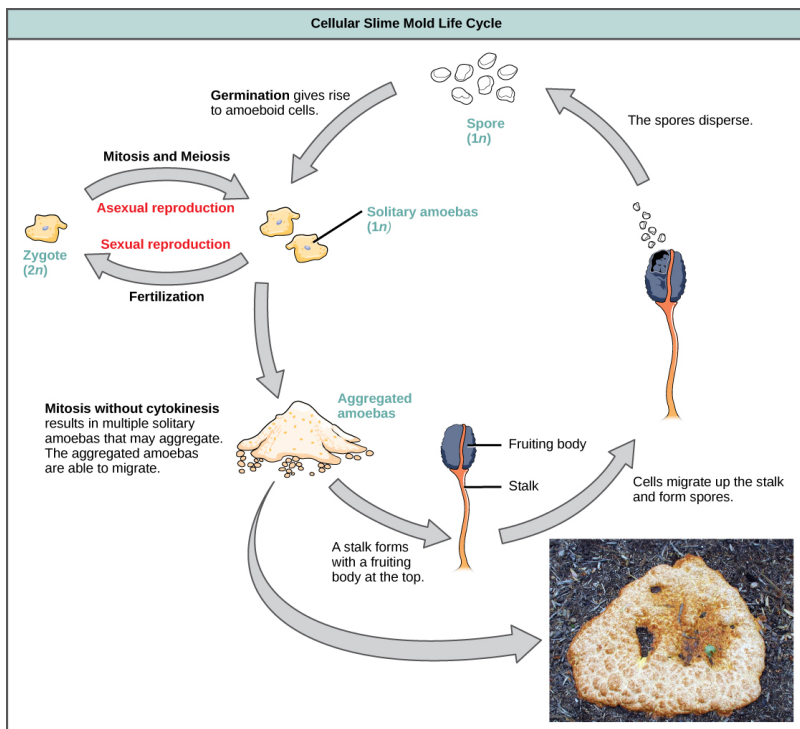
A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types.

Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage ([[link](#)]). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.



The cellular slime molds function as independent amoeboid cells when nutrients are abundant ([link]). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.



Link to Learning



View this video to see the formation of a fruiting body by a cellular slime mold.

https://www.openstaxcollege.org/1/slime_mold

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Section Summary

The process of classifying protists into meaningful

groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

[\[link\]](#) Which of the following statements about *Paramecium* sexual reproduction is false?

1. The macronuclei are derived from micronuclei.
2. Both mitosis and meiosis occur during sexual reproduction.
3. The conjugate pair swaps macronuclei.
4. Each parent produces four daughter cells.

[\[link\]](#) Which of the following statements about the *Laminaria* life cycle is false?

1. $1n$ zoospores form in the sporangia.
2. The sporophyte is the $2n$ plant.
3. The gametophyte is diploid.
4. Both the gametophyte and sporophyte stages are multicellular.

[\[link\]](#) C

Review Questions

Which protist group exhibits mitochondrial remnants with reduced functionality?

1. slime molds
2. diatoms
3. parabasalids
4. dinoflagellates

C

Conjugation between two *Paramecia* produces

_____ total daughter cells.

1. 2
2. 4
3. 8
4. 16

C

What is the function of the raphe in diatoms?

1. locomotion
2. defense
3. capturing food
4. photosynthesis

A

What genus of protists appears to contradict the statement that unicellularity restricts cell size?

1. *Dictyostelium*
2. *Ulva*
3. *Plasmodium*
4. *Caulerpa*

D

Free Response

The chlorophyte (green algae) genera *Ulva* and *Caulerpa* both have macroscopic leaf-like and stem-like structures, but only *Ulva* species are considered truly multicellular. Explain why.

Unlike *Ulva*, protists in the genus *Caulerpa* actually are large, multinucleate, single cells. Because these organisms undergo mitosis without cytokinesis and lack cytoplasmic divisions, they cannot be considered truly multicellular.

Why might a light-sensing eyespot be ineffective for an obligate saprobe? Suggest an alternative organ for a saprobic protist.

By definition, an obligate saprobe lacks the ability to perform photosynthesis, so it cannot directly obtain nutrition by searching for light. Instead, a chemotactic mechanism that senses the odors released during decay might be a more effective sensing organ for a saprobe.

Glossary

biological carbon pump

process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence

generation and emission of light by an organism, as in dinoflagellates

contractile vacuole

vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming

movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome

organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast

mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome

nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton

diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe

slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test

porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

Characteristics of Fungi

By the end of this section, you will be able to:

- List the characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi

Although humans have used yeasts and mushrooms since prehistoric times, until recently, the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, arose mostly sessile and seemingly rooted in place. They possess a stem-like structure similar to plants, as well as having a root-like fungal mycelium in the soil. In addition, their mode of nutrition was poorly understood. Progress in the field of fungal biology was the result of **mycology**: the scientific study of fungi. Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome demonstrates that fungi are more closely related to animals than plants. They are a polyphyletic group of organisms that share characteristics, rather than sharing a single common ancestor.

Mycologist

Mycologists are biologists who study fungi.

Mycology is a branch of microbiology, and many mycologists start their careers with a degree in microbiology. To become a mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are minimally necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the world, or the deadly epidemic called white nose syndrome, which is decimating bats in the Eastern United States.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests.

Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good understanding of fungal physiology routinely work

in the food technology industry. Oenology, the science of wine making, relies not only on the knowledge of grape varieties and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America. (credit: Christine Majul) *Candida albicans* is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell) The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC) Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae*

shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches ([\[link\]](#)). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

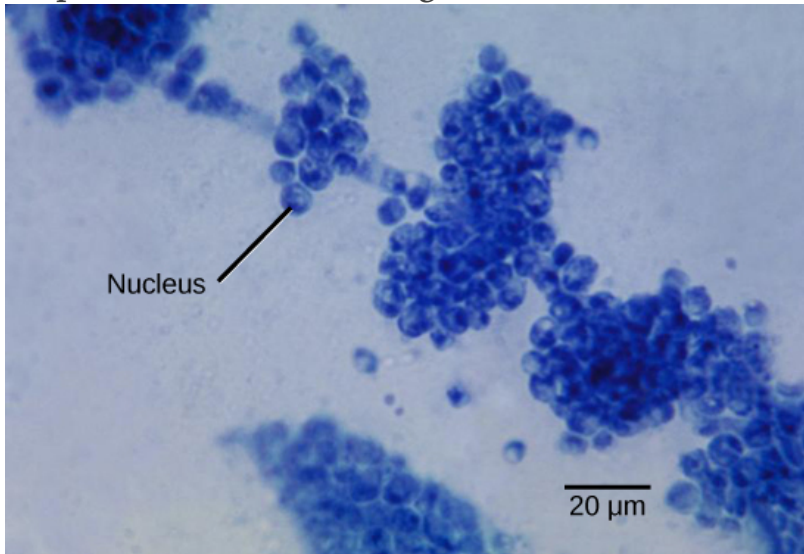


Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive Phylum Chytridiomycota.

Growth

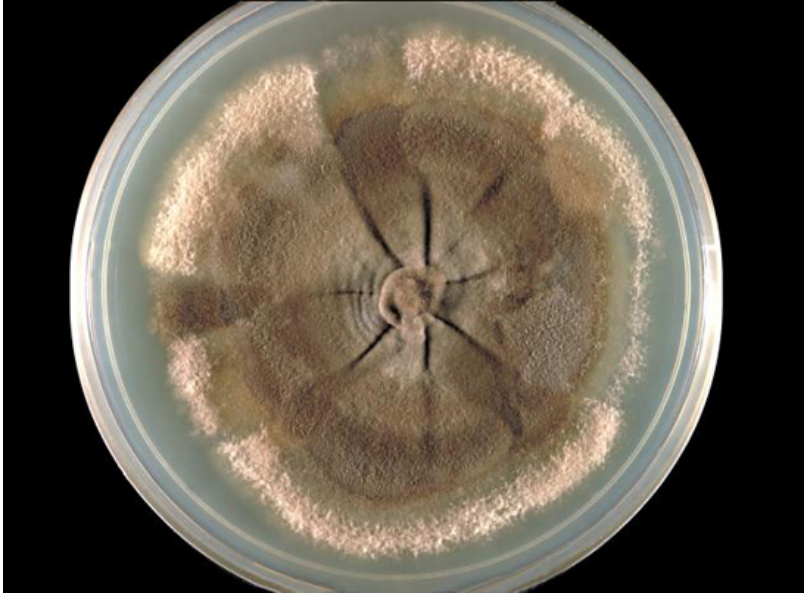
The vegetative body of a fungus is a unicellular or multicellular **thallus**. Dimorphic fungi can change

from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi ([\[link\]](#)).

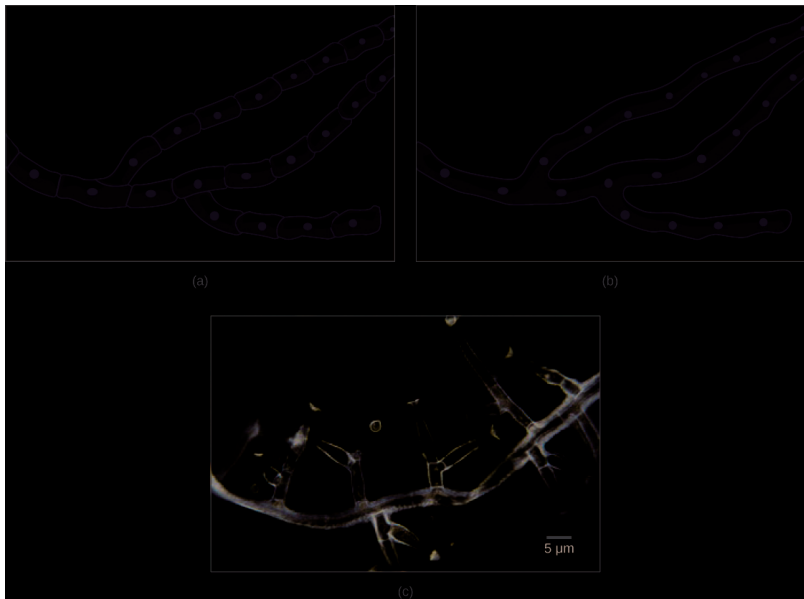


Most fungi are multicellular organisms. They display two distinct morphological stages: the vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, **hypha**), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a **mycelium** ([\[link\]](#)). It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being “the fungus humongous.” The

giant *Armillaria solidipes* (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.



Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) ([link]a, c). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as **coenocytic hyphae** ([link]b).



Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirement. Most fungi are **obligate aerobes**, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are **obligate anaerobes**, in that they only use anaerobic respiration because oxygen will disrupt their metabolism or kill them. Yeasts are intermediate, being **facultative anaerobes**. This means that they grow best in the presence of oxygen using aerobic respiration, but can survive using anaerobic respiration when oxygen is not available. The alcohol produced from yeast fermentation is used in wine and beer production.

Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen, rather than starch, as found in plants.

Fungi are mostly **saprobies** (saprophyte is an equivalent term): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi

can be used to break down diesel oil and polycyclic aromatic hydrocarbons (PAHs). Other species take up heavy metals, such as cadmium and lead.

Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete's foot and candidiasis (thrush) are medically important fungal infections in humans. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called **haustoria**. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host, release digestive enzymes within the host's body, and absorb the digested nutrients.

The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation) The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. *Histoplasma* primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal

disease. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell) Fungi may have both asexual and sexual stages of reproduction. This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while the so-called imperfect fungi reproduce only asexually (by mitosis).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth ([link](#)).



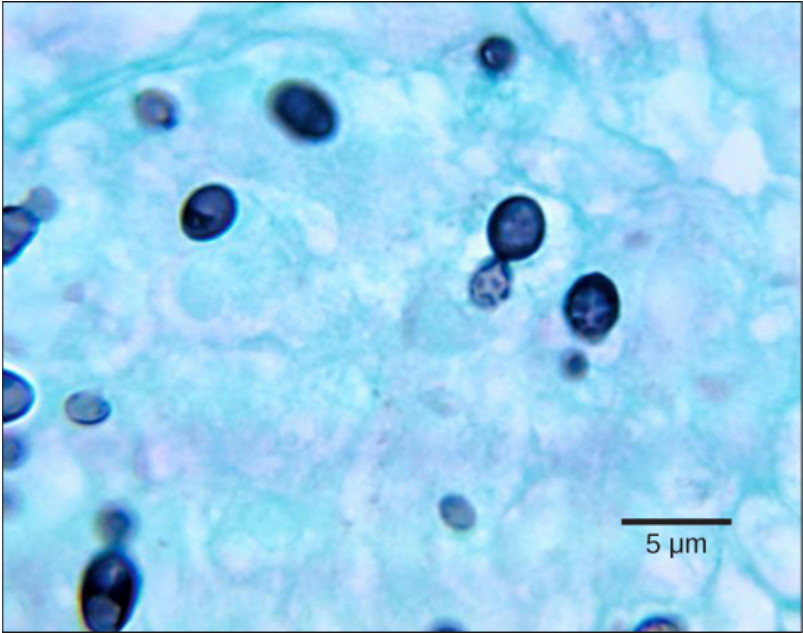
(a)



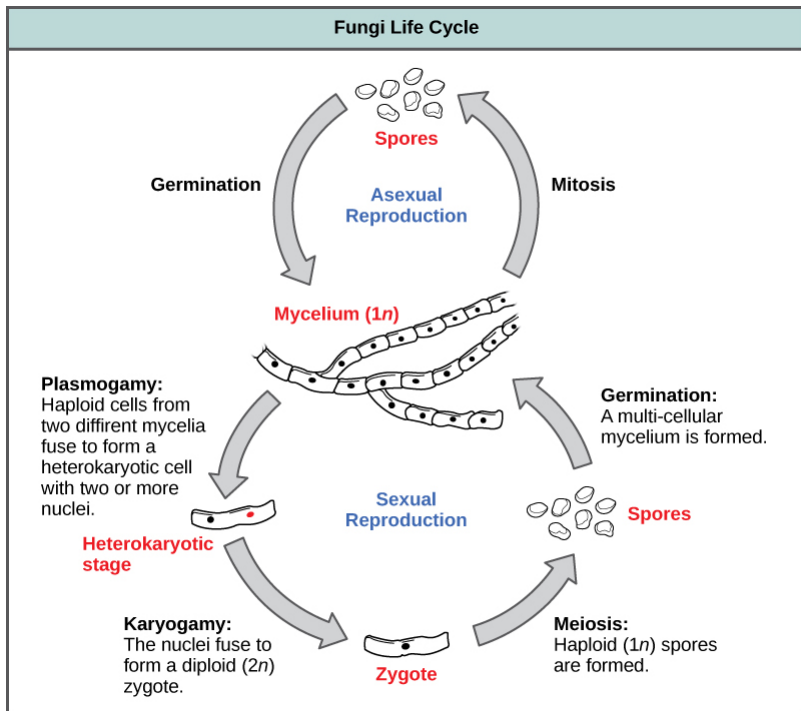
(b)

Asexual Reproduction

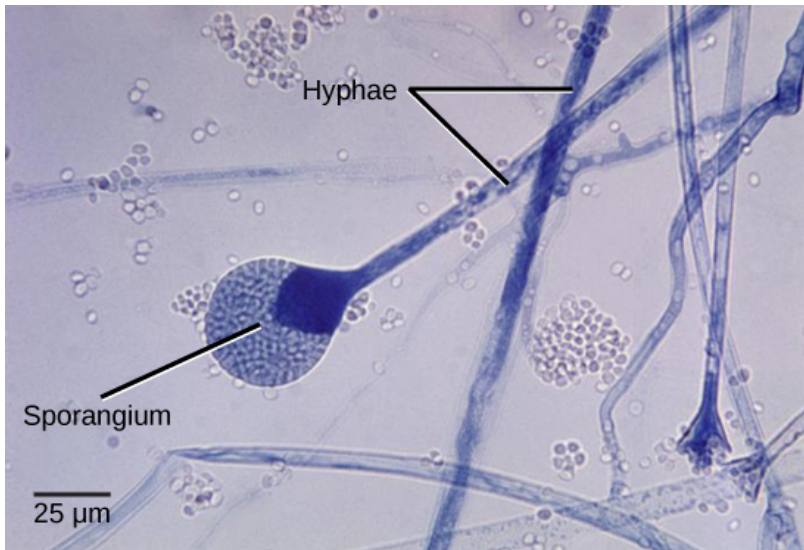
Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell ([\[link\]](#)).



The most common mode of asexual reproduction is through the formation of asexual spores, which are produced by one parent only (through mitosis) and are genetically identical to that parent ([\[link\]](#)). Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus either outside or within a special reproductive sac called a **sporangium**.



There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium ([link](#)).



Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages ([link]). First, during **plasmogamy** (literally, “marriage or union of cytoplasm”), two haploid cells fuse, leading to a dikaryotic stage where two haploid nuclei coexist in a single cell. During

karyogamy (“nuclear marriage”), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.

Link to Learning



Review the characteristics of fungi by visiting this [interactive site](#) from Wisconsin-online.

Section Summary

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic

pigments such as chlorophyll, nor organelles such as chloroplasts. Because fungi feed on decaying and dead matter, they are saprobes. Fungi are important decomposers that release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus, which is called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts, or develop a network of filaments called a mycelium, which is often described as mold. Most species multiply by asexual and sexual reproductive cycles and display an alternation of generations. Another group of fungi do not have a sexual cycle. Sexual reproduction involves plasmogamy (the fusion of the cytoplasm), followed by karyogamy (the fusion of nuclei). Meiosis regenerates haploid individuals, resulting in haploid spores.

Review Questions

Which polysaccharide is usually found in the cell wall of fungi?

1. starch
 2. glycogen
 3. chitin
 4. cellulose
-

C

Which of these organelles is not found in a fungal cell?

1. chloroplast
2. nucleus
3. mitochondrion
4. Golgi apparatus

A

The wall dividing individual cells in a fungal filament is called a

1. thallus
2. hypha
3. mycelium
4. septum

D

During sexual reproduction, a homothallic mycelium contains

1. all septated hyphae
2. all haploid nuclei

- 3. both mating types
 - 4. none of the above
-

C

Free Response

What are the evolutionary advantages for an organism to reproduce both asexually and sexually?

Asexual reproduction is fast and best under favorable conditions. Sexual reproduction allows the recombination of genetic traits and increases the odds of developing new adaptations better suited to a changed environment.

Compare plants, animals, and fungi, considering these components: cell wall, chloroplasts, plasma membrane, food source, and polysaccharide storage. Be sure to indicate fungi's similarities and differences to plants and animals.

Animals have no cell walls; fungi have cell walls containing chitin; plants have cell walls containing cellulose. Chloroplasts are absent in both animals and fungi but are present in plants. Animal plasma membranes are stabilized with cholesterol, while fungi plasma membranes are stabilized with ergosterol, and plant plasma membranes are stabilized with phytosterols. Animals obtain N and C from food sources via internal digestion. Fungi obtain N and C from food sources via external digestion. Plants obtain organic N from the environment or through symbiotic N-fixing bacteria; they obtain C from photosynthesis. Animals and fungi store polysaccharides as glycogen, while plants store them as starch.

Glossary

coenocytic hypha

single hypha that lacks septa and contains many nuclei

facultative anaerobes

organisms that can perform both aerobic and anaerobic respiration and can survive in oxygen-rich and oxygen-poor environment

haustoria

modified hyphae on many parasitic fungi that penetrate the tissues of their hosts, release

digestive enzymes, and/or absorb nutrients
from the host

heterothallic

describes when only one mating type is
present in an individual mycelium

homothallic

describes when both mating types are present
in mycelium

hypha

fungus filament composed of one or more cells

karyogamy

fusion of nuclei

mycelium

mass of fungal hyphae

mycology

scientific study of fungi

obligate aerobes

organisms, such as humans, that must
perform aerobic respiration to survive

obligate anaerobes

organisms that only perform anaerobic
respiration and often cannot survive in the
presence of oxygen

plasmogamy

fusion of cytoplasm

saprobe

organism that derives nutrients from decaying organic matter; also saprophyte

septa

cell wall division between hyphae

sporangium

reproductive sac that contains spores

thallus

vegetative body of a fungus

yeast

general term used to describe unicellular fungi

Classifications of Fungi

By the end of this section, you will be able to:

- Classify fungi into the five major phyla
- Describe each phylum in terms of major representative species and patterns of reproduction

The kingdom Fungi contains five major phyla that were established according to their mode of sexual reproduction or using molecular data. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, are placed for convenience in a sixth group called a “form phylum”. Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a part of RNA) continue to show new and different relationships between the various categories of fungi.

The five true phyla of fungi are the Chytridiomycota (Chytrids), the Zygomycota (conjugated fungi), the Ascomycota (sac fungi), the Basidiomycota (club fungi) and the recently described Phylum Glomeromycota. An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use.

Note: “-mycota” is used to designate a phylum while “-mycetes” formally denotes a class or is used

informally to refer to all members of the phylum.

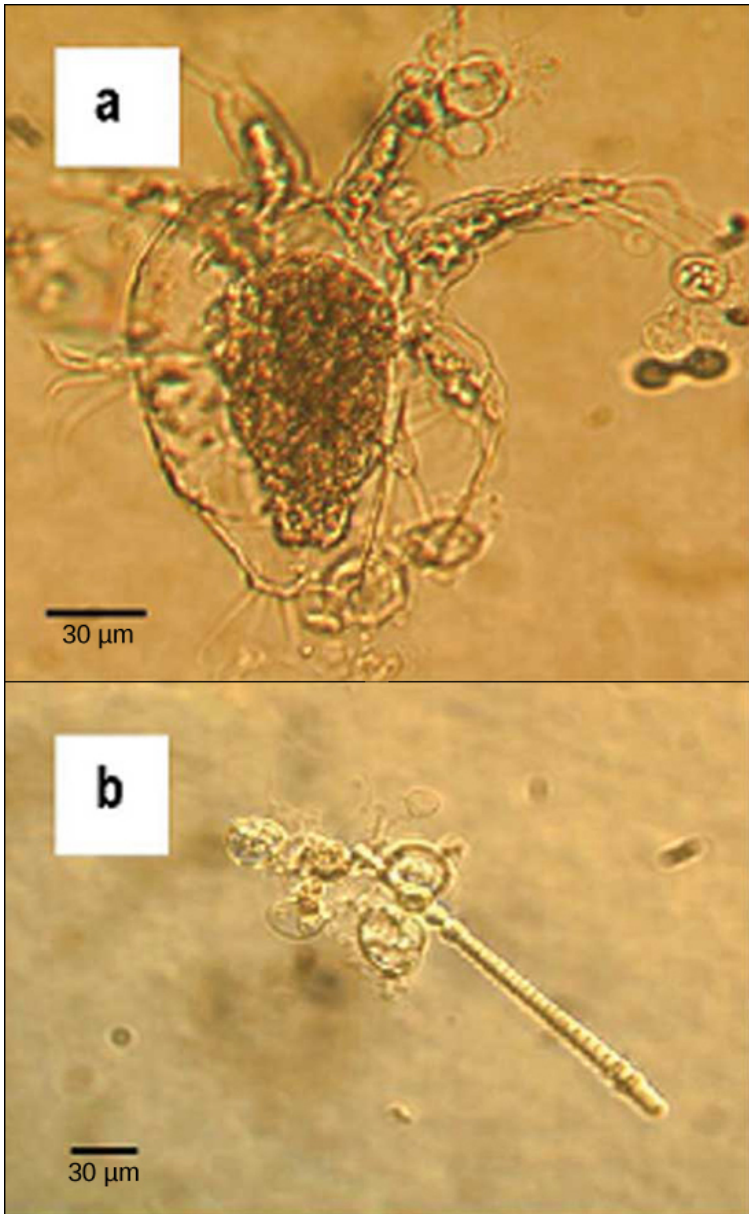
The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work by Johnson ML, Speare R., CDC)

Chytridiomycota: The Chytrids

The only class in the Phylum Chytridiomycota is the **Chytridiomycetes**. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They produce gametes and diploid zoospores that swim with the help of a single flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians ([\[link\]](#)), while

others are saprobes. The chytrid species *Allomyces* is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.



Zygomycetes have asexual and sexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygospore. Sporangia grow at the end of stalks, which appear as (a) white

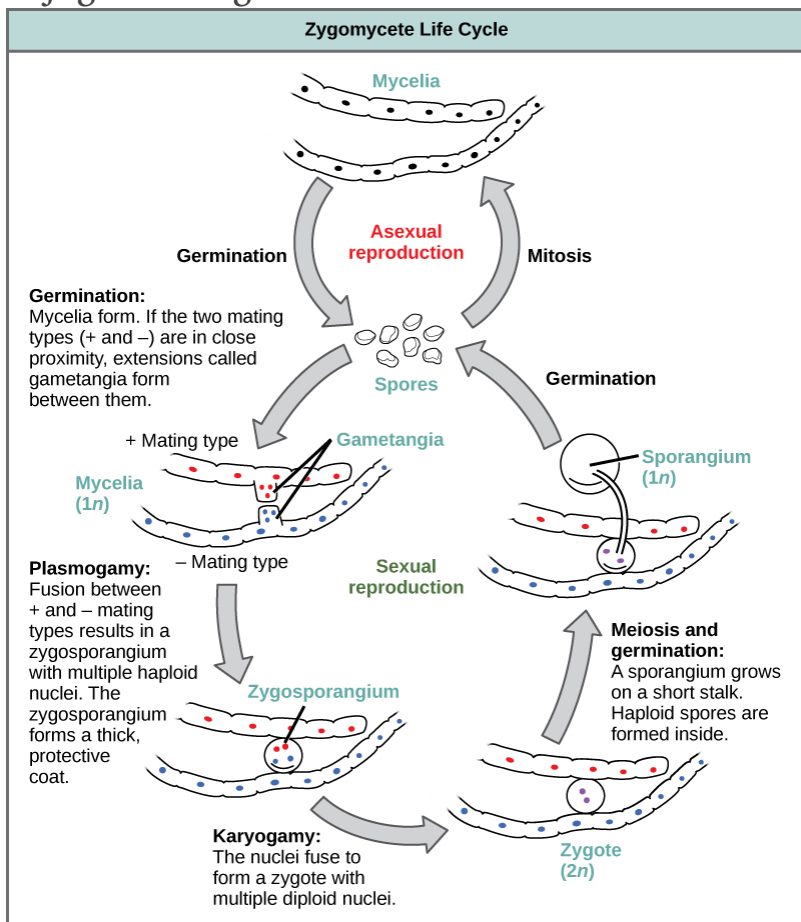
fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

Zygomycota: The Conjugated Fungi

The zygomycetes are a relatively small group of fungi belonging to the Phylum **Zygomycota**. They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. Most species are saprobes, living off decaying organic material; a few are parasites, particularly of insects. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores ([\[link\]](#)). The black tips of bread mold are the swollen sporangia packed with black spores ([\[link\]](#)). When spores land on a suitable substrate, they germinate and produce a new mycelium. Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type -) must be in close proximity for gametangia from the hyphae to be produced and fuse, leading to

karyogamy. The developing diploid **zygospores** have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi”.





(a)



(b)

The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

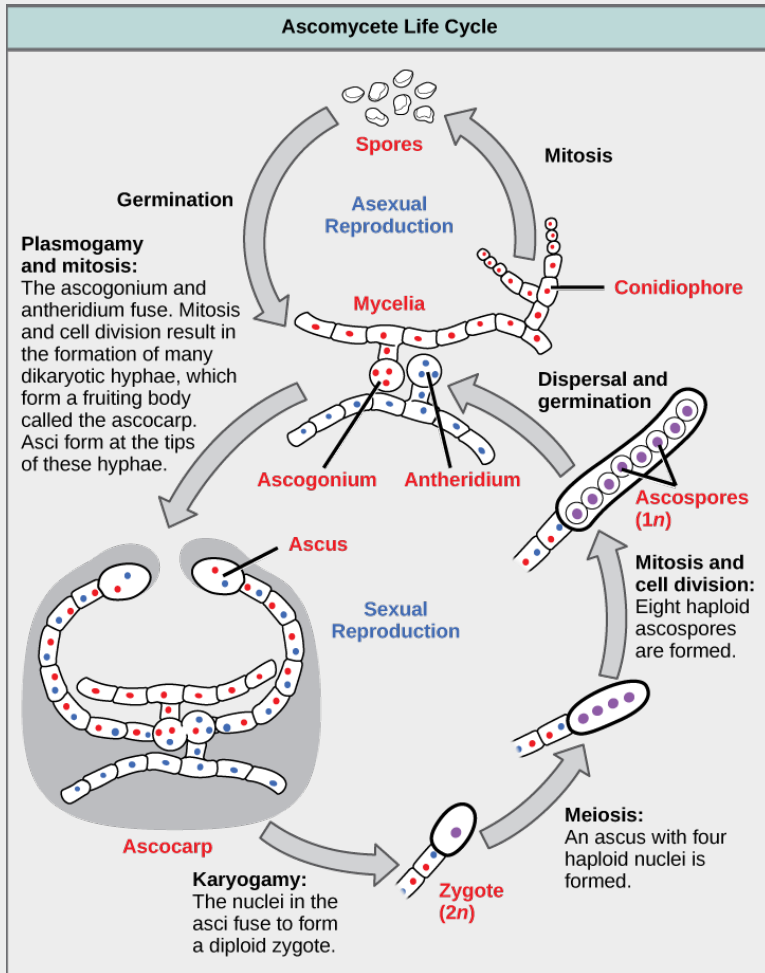
Ascomycota: The Sac Fungi

The majority of known fungi belong to the Phylum **Ascomycota**, which is characterized by the formation of an **ascus** (plural, **asci**), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly; they also produce poisonous secondary metabolites that make crops

unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores ([\[link\]](#)). Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains ([\[link\]](#)). The “male” strain produces an antheridium and the “female” strain develops an ascogonium. At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the “male” strain and one from the “female” strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy. During sexual reproduction, thousands of asci fill a fruiting body called the **ascocarp**. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia ([\[link\]](#)).

The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

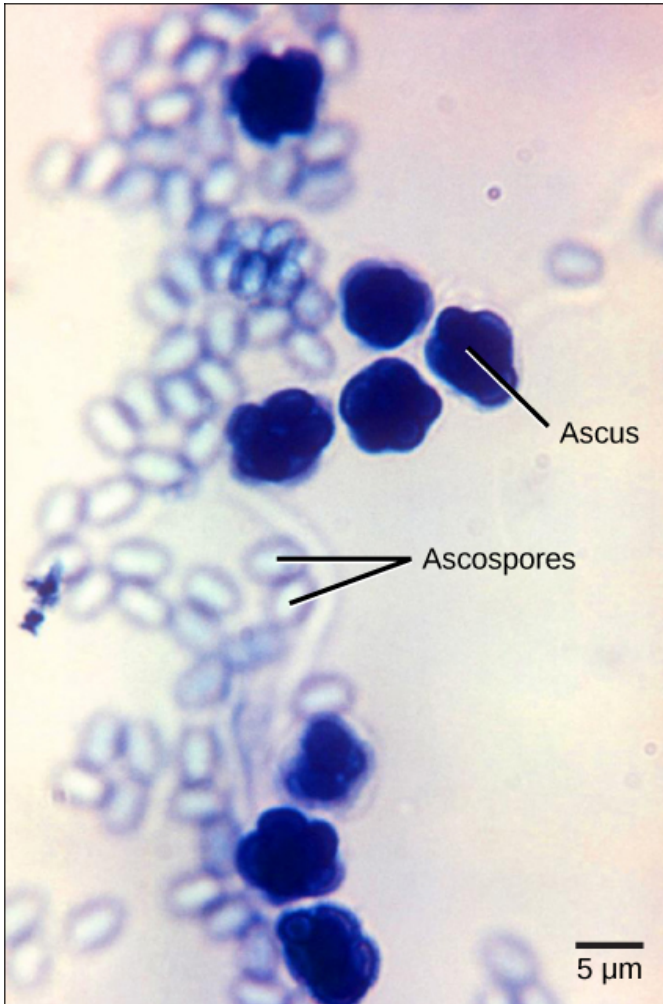


Which of the following statements is true?

1. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
2. A diploid ascus that forms in the ascocarp

undergoes karyogamy, meiosis, and mitosis to form eight ascospores.

3. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
4. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.



The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring.” The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center and leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen.

(Credit: "Cropcircles"/Wikipedia Commons)]

Basidiomycota: The Club Fungi

The fungi in the Phylum **Basidiomycota** are easily recognizable under a light microscope by their club-shaped fruiting bodies called **basidia** (singular, **basidium**), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn ([\[link\]](#)). These mushroom-producing basidiomycetes are sometimes referred to as “gill fungi” because of the presence of gill-like structures on the underside of the cap. The “gills” are actually compacted hyphae on which the basidia are borne. This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens; toadstools, and shelf fungi stacked on tree trunks. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.

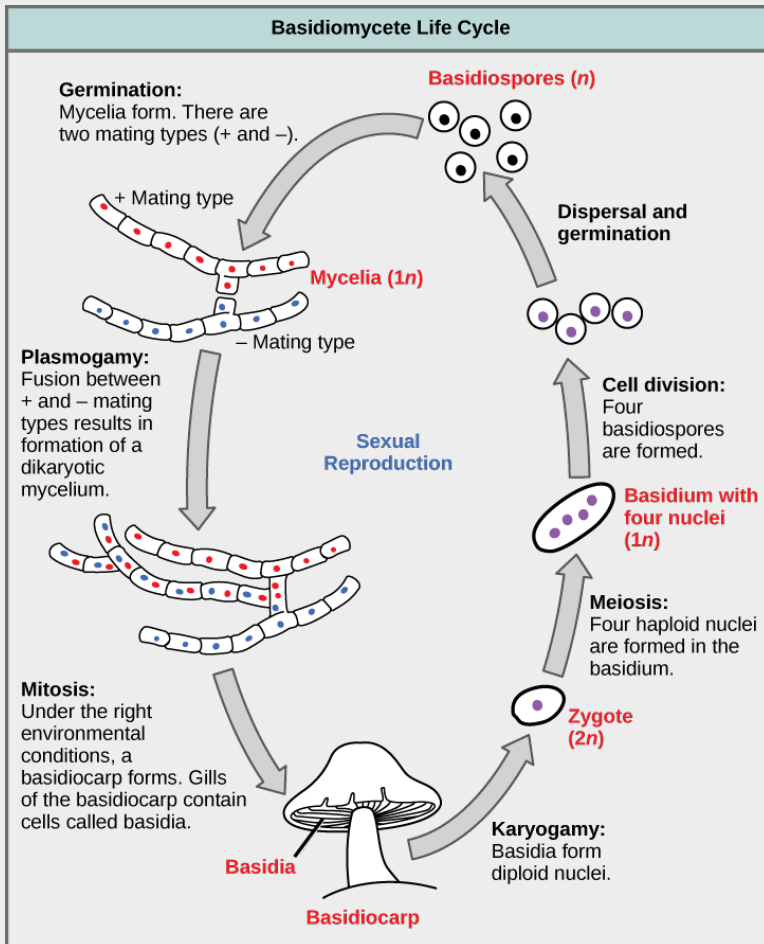


The lifecycle of basidiomycetes includes alternation of generations ([\[link\]](#)). Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomycetes lifecycle and it is the dominant stage. Eventually, the secondary mycelium generates a **basidiocarp**, which is a

fruiting body that protrudes from the ground—this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

Art Connection

The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.



Which of the following statements is true?

1. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
2. The result of the plasmogamy step is four basidiospores.
3. Karyogamy results directly in the formation of mycelia.
4. A basidiocarp is the fruiting body of a

mushroom-producing fungus.

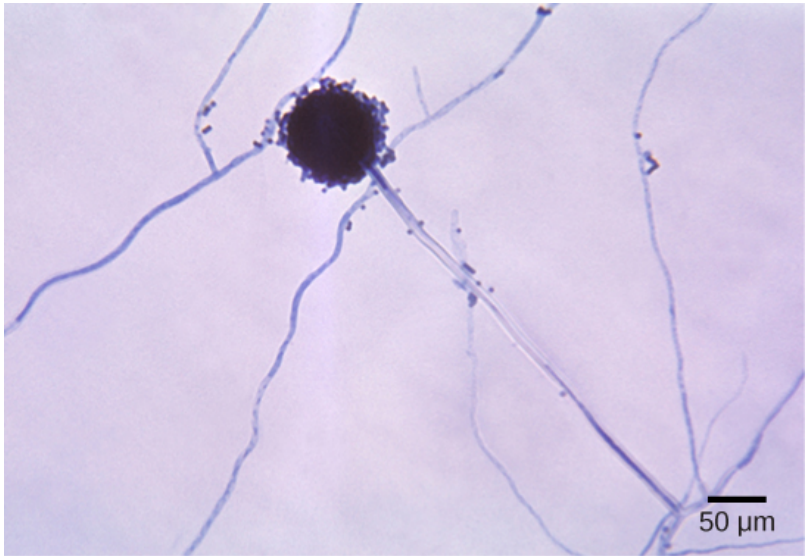
Aspergillus niger is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Asexual Ascomycota and Basidiomycota

Imperfect fungi—those that do not display a sexual phase—use to be classified in the form phylum **Deuteromycota**, , a classification group no longer used in the present, ever-developing classification of organisms. While Deuteromycota use to be a classification group, recent molecular analysis has shown that the members classified in this group belong to the Ascomycota or the Basidiomycota classifications. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other members. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.

Reproduction of the fungi in this group is strictly asexual and occurs mostly by production of asexual

conidiospores ([\[link\]](#)). Some hyphae may recombine and form heterokaryotic hyphae. Genetic recombination is known to take place between the different nuclei.



The fungi in this group have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi killed the bacterial growth surrounding it. Other fungi in this group cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

Glomeromycota

The **Glomeromycota** is a newly established phylum which comprises about 230 species that all live in close association with the roots of trees. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that all members of this family form **arbuscular mycorrhizae**: the hyphae interact with the root cells forming a mutually beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

Section Summary

Chytridiomycota (chytrids) are considered the most primitive group of fungi. They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called zoospores.

Zygomycota (conjugated fungi) produce non-septated hyphae with many nuclei. Their hyphae fuse during sexual reproduction to produce a zygospore in a zygosporangium. Ascomycota (sac fungi) form spores in sacs called asci during sexual reproduction. Asexual reproduction is their most common form of reproduction. Basidiomycota (club fungi) produce showy fruiting bodies that contain basidia in the form of clubs. Spores are stored in the basidia. Most familiar mushrooms belong to this division. Fungi that have no known sexual cycle were classified in the form phylum Deuteromycota, which the present classification puts in the phyla Ascomycota and Basidiomycota. Glomeromycota form tight associations (called mycorrhizae) with the roots of plants.

Art Connections

[\[link\]](#) Which of the following statements is true?

1. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
2. A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.

3. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
4. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.

[\[link\]](#) A

[\[link\]](#) Which of the following statements is true?

1. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
2. The result of the plasmogamy step is four basidiospores.
3. Karyogamy results directly in the formation of mycelia.
4. A basidiocarp is the fruiting body of a mushroom-producing fungus.

[\[link\]](#) D

Review Questions

The most primitive phylum of fungi is the _____.

1. Chytridiomycota
2. Zygomycota
3. Glomeromycota
4. Ascomycota

A

Members of which phylum produce a club-shaped structure that contains spores?

1. Chytridiomycota
2. Basidiomycota
3. Glomeromycota
4. Ascomycota

B

Members of which phylum establish a successful symbiotic relationship with the roots of trees?

1. Ascomycota
2. Deuteromycota
3. Basidiomycota
4. Glomeromycota

D

The fungi that do not reproduce sexually use to be classified as _____.

1. Ascomycota
2. Deuteromycota
3. Basidiomycota
4. Glomeromycota

B

Free Response

What is the advantage for a basidiomycete to produce a showy and fleshy fruiting body?

By ingesting spores and disseminating them in the environment as waste, animals act as agents of dispersal. The benefit to the fungus outweighs the cost of producing fleshy fruiting bodies.

For each of the four groups of perfect fungi

(Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota), compare the body structure and features, and provide an example.

Chytridiomycota (Chytrids) may have a unicellular or multicellular body structure; some are aquatic with motile spores with flagella; an example is the *Allomyces*. Zygomycota (conjugated fungi) have a multicellular body structure; features include zygospores and presence in soil; examples are bread and fruit molds. Ascomycota (sac fungi) may have unicellular or multicellular body structure; a feature is sexual spores in sacs (asci); examples include the yeasts used in bread, wine, and beer production. Basidiomycota (club fungi) have multicellular bodies; features includes sexual spores in the basidiocarp (mushroom) and that they are mostly decomposers; mushroom-producing fungi are an example.

Glossary

Arbuscular mycorrhizae

mycorrhizae commonly involving
Glomeromycetes in which the fungal hyphae
penetrate the cell walls of the plant root cells
(but not the cell membranes)

ascocarp

fruiting body of ascomycetes

Ascomycota

(also, sac fungi) phylum of fungi that store spores in a sac called ascus

basidiocarp

fruiting body that protrudes from the ground and bears the basidia

Basidiomycota

(also, club fungi) phylum of fungi that produce club-shaped structures (basidia) that contain spores

basidium

club-shaped fruiting body of basidiomycetes

Chytridiomycota

(also, chytrids) primitive phylum of fungi that live in water and produce gametes with flagella

Deuteromycota

former form phylum of fungi that do not have a known sexual reproductive cycle (presently members of two phyla: Ascomycota and Basidiomycota)

Ectomycorrhizae

mycorrhizae in which the fungal hyphae do

not penetrate the root cells of the plant

Glomeromycota

phylum of fungi that form symbiotic relationships with the roots of trees

mold

tangle of visible mycelia with a fuzzy appearance

Zygomycota

(also, conjugated fungi) phylum of fungi that form a zygote contained in a zygospore

zygospore

structure with thick cell wall that contains the zygote in zygomycetes

The Plant Kingdom

By the end of this section, you will be able to:

- Describe the major characteristics of the plant kingdom
- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize land

Plants are a large and varied group of organisms. There are close to 300,000 species of catalogued plants.^[footnote] Of these, about 260,000 are plants that produce seeds. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom. The plant kingdom contains mostly photosynthetic organisms; a few parasitic forms have lost the ability to photosynthesize. The process of photosynthesis uses chlorophyll, which is located in organelles called chloroplasts. Plants possess cell walls containing cellulose. Most plants reproduce sexually, but they also have diverse methods of asexual reproduction. Plants exhibit indeterminate growth, meaning they do not have a final body form, but continue to grow body mass until they die.

A.D. Chapman (2009) *Numbers of Living Species in Australia and the World*. 2nd edition. A Report for the Australian Biological Resources Study.

Australian Biodiversity Information Services, Toowoomba, Australia. Available online at <http://www.environment.gov.au/biodiversity/abrs/>

[publications/other/species-numbers/2009/04-03-groups-plants.html](#). Alternation of generations between the haploid ($1n$) gametophyte and diploid ($2n$) sporophyte is shown. (credit: modification of work by Peter Coxhead) This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons) This life cycle of a moss shows alternation of generations with a dominant gametophyte stage. (credit: modification of work by Mariana Ruiz Villareal) This apple seedling is an example of a plant in which the apical meristem gives rise to new shoots and root growth.

Plant Adaptations to Life on Land

As organisms adapt to life on land, they have to contend with several challenges in the terrestrial environment. Water has been described as “the stuff of life.” The cell’s interior—the medium in which most small molecules dissolve and diffuse, and in which the majority of the chemical reactions of metabolism take place—is a watery soup. Desiccation, or drying out, is a constant danger for an organism exposed to air. Even when parts of a plant are close to a source of water, their aerial structures are likely to dry out. Water provides buoyancy to organisms that live in aquatic habitats. On land, plants need to develop structural support

in air—a medium that does not give the same lift. Additionally, the male gametes must reach the female gametes using new strategies because swimming is no longer possible. Finally, both gametes and zygotes must be protected from drying out. The successful land plants evolved strategies to deal with all of these challenges, although not all adaptations appeared at once. Some species did not move far from an aquatic environment, whereas others left the water and went on to conquer the driest environments on Earth.

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. On land, the spectral quality of light absorbed by the photosynthetic pigment, chlorophyll, is not filtered out by water or competing photosynthetic species in the water column above. Second, carbon dioxide is more readily available because its concentration is higher in air than in water. Additionally, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened the well-being of plants. This situation changed as animals emerged from the water and found abundant sources of nutrients in the established flora. In turn, plants evolved strategies to deter predation: from spines and thorns to toxic chemicals.

The early land plants, like the early land animals,

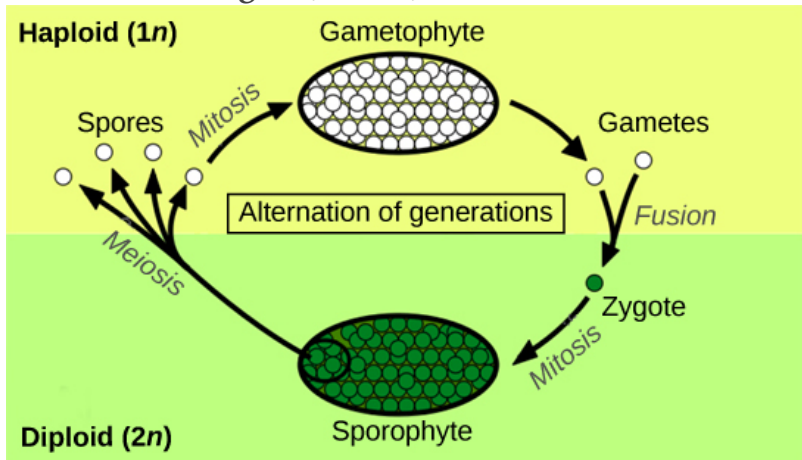
did not live far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is drought tolerance. Mosses, for example, can dry out to a brown and brittle mat, but as soon as rain makes water available, mosses will soak it up and regain their healthy, green appearance. Another strategy is to colonize environments with high humidity where droughts are uncommon. Ferns, an early lineage of plants, thrive in damp and cool places, such as the understory of temperate forests. Later, plants moved away from aquatic environments using resistance to desiccation, rather than tolerance. These plants, like the cactus, minimize water loss to such an extent they can survive in the driest environments on Earth.

In addition to adaptations specific to life on land, land plants exhibit adaptations that were responsible for their diversity and predominance in terrestrial ecosystems. Four major adaptations are found in many terrestrial plants: the alternation of generations, a sporangium in which spores are formed, a gametangium that produces haploid cells, and in vascular plants, apical meristem tissue in roots and shoots.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid

multicellular stages ([\[link\]](#)).



Haplontic refers to a life cycle in which there is a dominant haploid stage. **Diplontic** refers to a life cycle in which the diploid stage is the dominant stage, and the haploid chromosome number is only seen for a brief time in the life cycle during sexual reproduction. Humans are diplontic, for example. Most plants exhibit alternation of generations, which is described as **haplodiplontic**: the haploid multicellular form known as a gametophyte is followed in the development sequence by a multicellular diploid organism, the **sporophyte**. The **gametophyte** gives rise to the gametes, or reproductive cells, by mitosis. It can be the most obvious phase of the life cycle of the plant, as in the mosses, or it can occur in a microscopic structure, such as a pollen grain in the higher plants (the collective term for the vascular plants). The sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses,

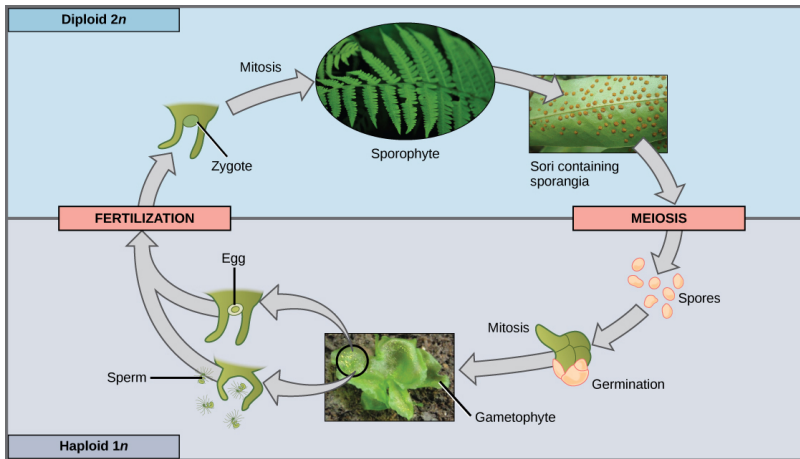
liverworts, and hornworts). Towering trees are the diplontic phase in the lifecycles of plants such as sequoias and pines.

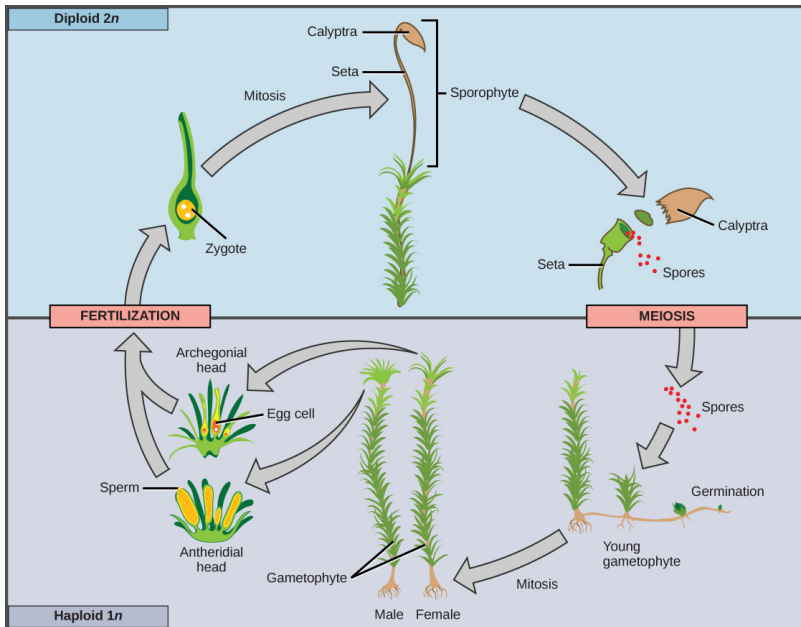
Sporangia in the Seedless Plants

The sporophyte of seedless plants is diploid and results from **syngamy** or the fusion of two gametes ([\[link\]](#)). The sporophyte bears the **sporangia** (singular, sporangium), organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel,” as it is a reproductive sac that contains spores. Inside the multicellular sporangia, the diploid sporocytes, or mother cells, produce haploid spores by meiosis, which reduces the $2n$ chromosome number to $1n$. The spores are later released by the sporangia and disperse in the environment. Two different types of spores are produced in land plants, resulting in the separation of sexes at different points in the life cycle. Seedless nonvascular plants (more appropriately referred to as “seedless nonvascular plants with a dominant gametophyte phase”) produce only one kind of spore, and are called **homosporous**. After germinating from a spore, the gametophyte produces both male and female **gametangia**, usually on the same individual. In contrast, **heterosporous** plants produce two morphologically different types of spores. The male spores are called microspores because of their smaller size; the comparatively larger megaspores will develop into

the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

When the haploid spore germinates, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte or vegetative form, and the cycle begins anew ([\[link\]](#) and [\[link\]](#)).





The spores of seedless plants and the pollen of seed plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. This substance is characterized by long chains of organic molecules related to fatty acids and carotenoids, and gives most pollen its yellow color. Sporopollenin is unusually resistant to chemical and biological degradation. Its toughness explains the existence of well-preserved fossils of pollen. Sporopollenin was once thought to be an innovation of land plants; however, the green algae *Coleochaetes* is now known to form spores that contain sporopollenin.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental

hazards. In both seedless and seed plants, the female gametophyte provides nutrition, and in seed plants, the embryo is also protected as it develops into the new generation of sporophyte.

Gametangia in the Seedless Plants

Gametangia (singular, gametangium) are structures on the gametophytes of seedless plants in which gametes are produced by mitosis. The male gametangium, the antheridium, releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the archegonia, the female gametangium. The embryo develops inside the archegonium as the sporophyte.

Apical Meristems

The shoots and roots of plants increase in length through rapid cell division within a tissue called the **apical meristem** ([\[link\]](#)). The apical meristem is a cap of cells at the shoot tip or root tip made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the plant. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter

of stems and tree trunks. Apical meristems are an adaptation to allow vascular plants to grow in directions essential to their survival: upward to greater availability of sunlight, and downward into the soil to obtain water and essential minerals.



Plants have evolved various adaptations to life on land. (a) Early plants grew close to the ground, like this moss, to avoid desiccation. (b) Later plants developed a waxy cuticle to prevent desiccation. (c) To grow taller, like these maple trees, plants had to evolve new structural chemicals to strengthen their stems and vascular systems to transport water and minerals from the soil and nutrients from the leaves.

(d) Plants developed physical and chemical defenses to avoid being eaten by animals. (credit a, b: modification of work by Cory Zanker; credit c: modification of work by Christine Cimala; credit d: modification of work by Jo Naylor)

Additional Land Plant Adaptations

As plants adapted to dry land and became independent of the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow above a few inches off the ground, and on these low mats, they competed for light. By evolving a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). The evolution of vascular tissue for the distribution of water and solutes was a necessary prerequisite for plants to evolve larger bodies. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals taken from the soil up to the shoot; phloem transports food derived from photosynthesis throughout the entire plant. The root system that evolved to take up water and minerals also anchored the increasingly taller shoot in the soil.

In land plants, a waxy, waterproof cover called a cuticle coats the aerial parts of the plant: leaves and

stems. The cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. Stomata, or pores, that open and close to regulate traffic of gases and water vapor therefore appeared in plants as they moved into drier habitats.

Plants cannot avoid predatory animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can cause severe diseases and even death.

Additionally, as plants coevolved with animals, sweet and nutritious metabolites were developed to lure animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been coevolving with animal associates for hundreds of millions of years ([\[link\]](#)).



(a)



(b)



(c)



(d)

Evolution in Action

Paleobotany

How organisms acquired traits that allow them to colonize new environments, and how the contemporary ecosystem is shaped, are fundamental questions of evolution. Paleobotany addresses these questions by specializing in the study of extinct plants. Paleobotanists analyze specimens retrieved from field studies, reconstituting the morphology of organisms that have long disappeared. They trace the evolution of plants by following the modifications in plant

morphology, and shed light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Fossils are formed when organisms are trapped in sediments or environments where their shapes are preserved ([\[link\]](#)). Paleobotanists determine the geological age of specimens and the nature of their environment using the geological sediments and fossil organisms surrounding them. The activity requires great care to preserve the integrity of the delicate fossils and the layers in which they are found.

One of the most exciting recent developments in paleobotany is the use of analytical chemistry and molecular biology to study fossils. Preservation of molecular structures requires an environment free of oxygen, since oxidation and degradation of material through the activity of microorganisms depend on the presence of oxygen. One example of the use of analytical chemistry and molecular biology is in the identification of oleanane, a compound that deters pests and which, up to this point, appears to be unique to flowering plants. Oleanane was recovered from sediments dating from the Permian, much earlier than the current dates given for the appearance of the first flowering plants. Fossilized nucleic acids—DNA and RNA—yield the most information. Their sequences are analyzed and compared to those of

living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For one, the chemical materials of interest degrade rapidly during initial isolation when exposed to air, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.

This fossil of a palm leaf (*Palmacites* sp.) discovered in Wyoming dates to about 40 million years ago.



This table shows the major divisions of plants.

The Major Divisions of Land Plants

Land plants are classified into two major groups according to the absence or presence of vascular tissue, as detailed in [\[link\]](#). Plants that lack vascular tissue formed of specialized cells for the transport of water and nutrients are referred to as **nonvascular plants**. The bryophytes, liverworts, mosses, and hornworts are seedless and nonvascular, and likely appeared early in land plant evolution. **Vascular plants** developed a network of cells that conduct water and solutes through the plant body. The first vascular plants appeared in the late Ordovician (461–444 million years ago) and were probably similar to lycophytes, which include club mosses (not to be confused with the mosses) and the pterophytes (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as seedless vascular plants. They do not produce seeds, which are embryos with their stored food reserves protected by a hard casing. The seed plants form the largest group of all existing plants and, hence, dominate the landscape. Seed plants include gymnosperms, most notably conifers, which produce “naked seeds,” and the most successful plants, the flowering plants, or angiosperms, which protect their seeds inside chambers at the center of a flower. The walls of these chambers later develop into fruits.

Embryophytes: The Land Plants						
Nonvascular Plants "Bryophytes"			Vascular Plants			
Liverworts	Hornworts	Mosses	Seedless Plants		Seed Plants	
			Lycophytes	Pterophytes	Gymno-sperms	Angio-sperms
			Club Mosses	Whisk Ferns		
			Quillworts	Horsetails		
			Spike Mosses	Ferns		

Section Summary

Land plants evolved traits that made it possible to colonize land and survive out of water. Adaptations to life on land include vascular tissues, roots, leaves, waxy cuticles, and a tough outer layer that protects the spores. Land plants include nonvascular plants and vascular plants. Vascular plants, which include seedless plants and plants with seeds, have apical meristems, and embryos with nutritional stores. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte and the diploid plant called a sporophyte; formation of haploid spores in a sporangium; and formation of gametes in a gametangium.

Multiple Choice

The land plants are probably descendants of which of these groups?

1. green algae
 2. red algae
 3. brown algae
 4. angiosperms
-

A

The event that leads from the haploid stage to the diploid stage in alternation of generations is _____.

1. meiosis
 2. mitosis
 3. fertilization
 4. germination
-

C

Moss is an example of which type of plant?

1. haplontic plant
 2. vascular plant
 3. diplontic plant
 4. seed plant
-

Free Response

What adaptations do plants have that allow them to survive on land?

The sporangium of plants protects the spores from drying out. Apical meristems ensure that a plant is able to grow in the two directions required to acquire water and nutrients: up toward sunlight and down into the soil. The multicellular embryo is an important adaptation that improves survival of the developing plant in dry environments. The development of molecules that gave plants structural strength allowed them to grow higher on land and obtain more sunlight. A waxy cuticle prevents water loss from aerial surfaces.

Glossary

apical meristem

the growing point in a vascular plant at the tip of a shoot or root where cell division occurs

diplontic

describes a life cycle in which the diploid stage is the dominant stage

gametangium

(plural: gametangia) the structure within which gametes are produced

gametophyte

the haploid plant that produces gametes

haplodiplontic

describes a life cycle in which the haploid and diploid stages alternate; also known as an alternation of generations life cycle

haplontic

describes a life cycle in which the haploid stage is the dominant stage

heterosporous

having two kinds of spores that give rise to male and female gametophytes

homosporous

having one kind of spore that gives rise to gametophytes that give rise to both male and female gametes

nonvascular plant

a plant that lacks vascular tissue formed of specialized cells for the transport of water and

nutrients

sporangium

(plural: sporangia) the organ within which spores are produced

sporophyte

the diploid plant that produces spores

syngamy

the union of two gametes in fertilization

vascular plant

a plant in which there is a network of cells that conduct water and solutes through the organism

Green Algae: Precursors of Land Plants

By the end of this section, you will be able to:

- Describe the traits shared by green algae and land plants
- Explain the reasons why Charales are considered the closest relative to land plants
- Understand that current phylogenetic relationships are reshaped by comparative analysis of DNA sequences

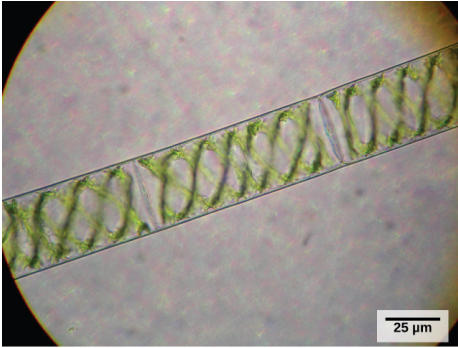
Chlorophyta include (a) *Spirogyra*, (b) desmids, (c) *Chlamydomonas*, and (d) *Ulva*. Desmids and *Chlamydomonas* are single-celled organisms, *Spirogyra* forms chains of cells, and *Ulva* forms colonies resembling leaves (credit b: modification of work by Derek Keats; credit c: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; credit d: modification of work by Holger Krisp; scale-bar data from Matt Russell)

Streptophytes

Until recently, all photosynthetic eukaryotes were considered members of the kingdom Plantae. The brown, red, and gold algae, however, have been reassigned to the Protista kingdom. This is because apart from their ability to capture light energy and fix CO₂, they lack many structural and biochemical traits that distinguish plants from protists. The

position of green algae is more ambiguous. Green algae contain the same carotenoids and chlorophyll *a* and *b* as land plants, whereas other algae have different accessory pigments and types of chlorophyll molecules in addition to chlorophyll *a*. Both green algae and land plants also store carbohydrates as starch. Cells in green algae divide along cell plates called phragmoplasts, and their cell walls are layered in the same manner as the cell walls of embryophytes. Consequently, land plants and closely related green algae are now part of a new monophyletic group called **Streptophyta**.

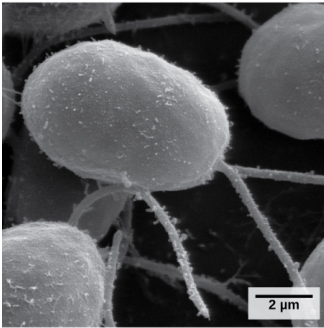
The remaining green algae, which belong to a group called Chlorophyta, include more than 7000 different species that live in fresh or brackish water, in seawater, or in snow patches. A few green algae even survive on soil, provided it is covered by a thin film of moisture in which they can live. Periodic dry spells provide a selective advantage to algae that can survive water stress. Some green algae may already be familiar, in particular *Spirogyra* and desmids. Their cells contain chloroplasts that display a dizzying variety of shapes, and their cell walls contain cellulose, as do land plants. Some green algae are single cells, such as *Chlorella* and *Chlamydomonas*, which adds to the ambiguity of green algae classification, because plants are multicellular. Other algae, like *Ulva* (commonly called sea lettuce), form colonies ([\[link\]](#)).



(a) *Spirogyra*



(b) Desmid



(c) *Chlamydomonas*



(d) *Ulva*

Reproduction of Green Algae

Green algae reproduce both asexually, by fragmentation or dispersal of spores, or sexually, by producing gametes that fuse during fertilization. In a single-celled organism such as *Chlamydomonas*, there is no mitosis after fertilization. In the multicellular *Ulva*, a sporophyte grows by mitosis after fertilization. Both *Chlamydomonas* and *Ulva* produce flagellated gametes.

The representative alga, *Chara*, is a noxious weed in Florida, where it clogs waterways. (credit: South

Charales

Green algae in the order Charales, and the coleochaetes (microscopic green algae that enclose their spores in sporopollenin), are considered the closest living relatives of embryophytes. The Charales can be traced back 420 million years. They live in a range of fresh water habitats and vary in size from a few millimeters to a meter in length. The representative species is *Chara* ([\[link\]](#)), often called muskgrass or skunkweed because of its unpleasant smell. Large cells form the thallus: the main stem of the alga. Branches arising from the nodes are made of smaller cells. Male and female reproductive structures are found on the nodes, and the sperm have flagella. Unlike land plants, Charales do not undergo alternation of generations in their lifecycle. Charales exhibit a number of traits that are significant in their adaptation to land life. They produce the compounds lignin and sporopollenin, and form plasmodesmata that connect the cytoplasm of adjacent cells. The egg, and later, the zygote, form in a protected chamber on the parent plant.



New information from recent, extensive DNA sequence analysis of green algae indicates that the Zygnematales are more closely related to the embryophytes than the Charales. The Zygnematales include the familiar genus *Spirogyra*. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between species will change. Clearly, plant biologists have not yet solved the mystery of the origin of land plants.

Section Summary

Green algae share more traits with land plants than other algae, according to structure and DNA

analysis. Charales form sporopollenin and precursors of lignin, phragmoplasts, and have flagellated sperm. They do not exhibit alternation of generations.

Review Questions

What characteristic of Charales would enable them to survive a dry spell?

1. sperm with flagella
2. phragmoplasts
3. sporopollenin
4. chlorophyll *a*

C

Which one of these characteristics is present in land plants and not in Charales?

1. alternation of generations
2. flagellated sperm
3. phragmoplasts
4. plasmodesmata

A

Free Response

To an alga, what is the main advantage of producing drought-resistant structures?

It allows for survival through periodic droughts and colonization of environments where the supply of water fluctuates.

Glossary

streptophytes

group that includes green algae and land plants

Bryophytes

By the end of this section, you will be able to:

- Identify the main characteristics of bryophytes
- Describe the distinguishing traits of liverworts, hornworts, and mosses
- Chart the development of land adaptations in the bryophytes
- Describe the events in the bryophyte lifecycle

Bryophytes are the group of plants that are the closest extant relative of early terrestrial plants. The first bryophytes (liverworts) most likely appeared in the Ordovician period, about 450 million years ago. Because of the lack of lignin and other resistant structures, the likelihood of bryophytes forming fossils is rather small. Some spores protected by sporopollenin have survived and are attributed to early bryophytes. By the Silurian period, however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

More than 25,000 species of bryophytes thrive in mostly damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They generally lack lignin and do not have actual tracheids (xylem cells specialized for

water conduction). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs—including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate—belong to the haploid organism or gametophyte. The sporophyte is barely noticeable. The gametes formed by bryophytes swim with a flagellum, as do gametes in a few of the tracheophytes. The sporangium—the multicellular sexual reproductive structure—is present in bryophytes and absent in the majority of algae. The bryophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

This 1904 drawing shows the variety of forms of Hepaticophyta. A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage. The life cycle of a typical liverwort is shown. (credit: modification of work by Mariana Ruiz Villareal)

Liverworts

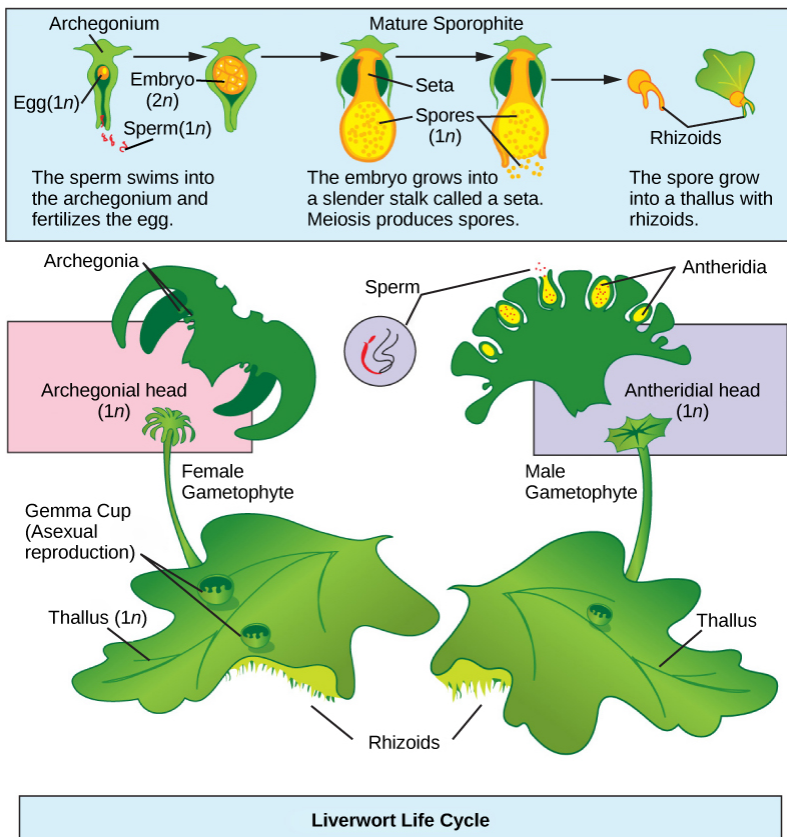
Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on Earth and diversified to more than 7000 existing species ([\[link\]](#)). Some gametophytes form lobate green structures, as seen in [\[link\]](#). The shape is similar to the lobes of the liver, and hence provides the origin of the name given to the phylum.





Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata, because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation. [\[link\]](#) represents the lifecycle of a liverwort. The cycle starts with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte. It will give rise, by meiosis, to

the next generation of spores. Liverwort plants can also reproduce asexually, by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the **gemmae**—small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus (shown in [\[link\]](#))—are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.



Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)
The alternation of generation in hornworts is shown.

(credit: modification of work by “Smith609”/
Wikimedia Commons based on original work by
Mariana Ruiz Villareal)

Hornworts

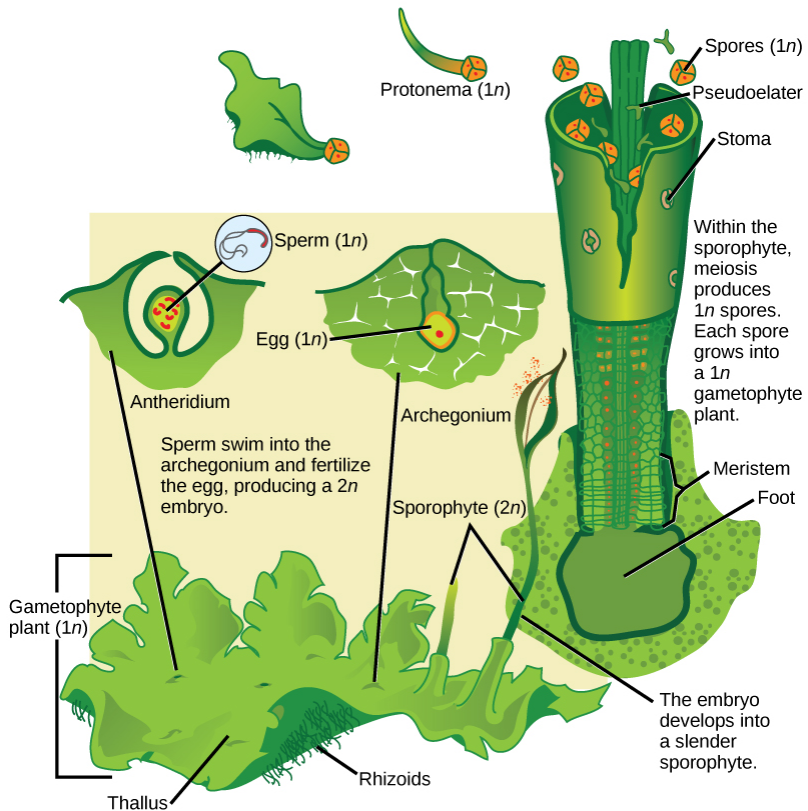
The **hornworts** (*Anthocerotophyta*) belong to the broad bryophyte group. They have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant ([link]).



Stomata appear in the hornworts and are abundant

on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.

The lifecycle of hornworts ([\[link\]](#)) follows the general pattern of alternation of generations. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. The zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in horsetails, the hornwort pseudoelaters are single-celled structures. The haploid spores germinate and give rise to the next generation of gametophyte.



This photograph shows the long slender stems, called setae, connected to capsules of the moss *Thamnobryum alopecurum*. (credit: modification of work by Hermann Schachner)

Mosses

More than 10,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a

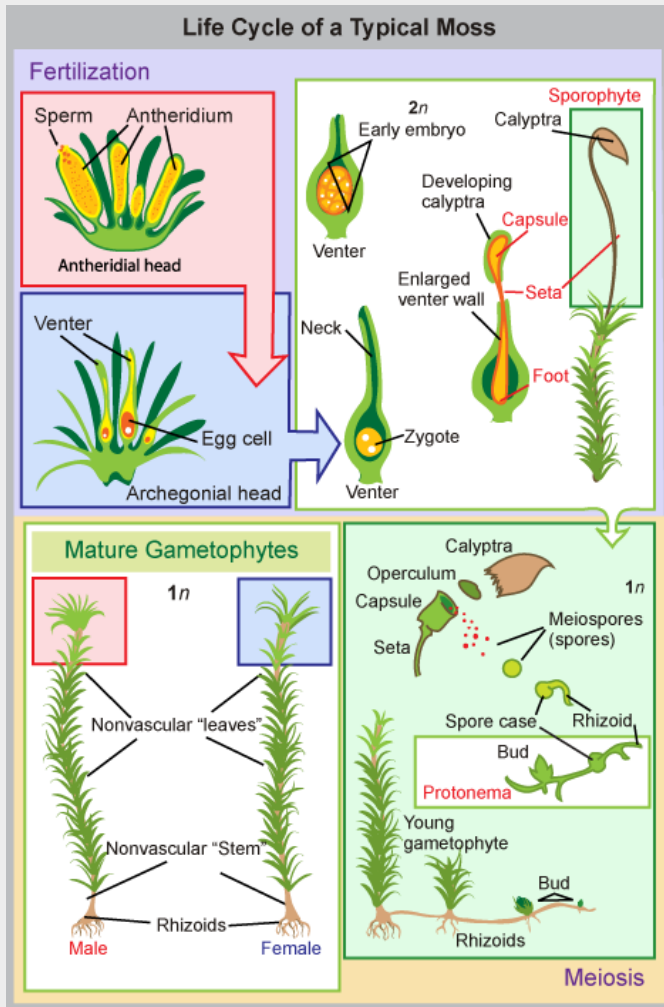
substrate without penetrating the frozen soil. Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts, so these salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the lifecycle. Green, flat structures—resembling true leaves, but lacking vascular tissue—are attached in a spiral to a central stalk. The plants absorb water and nutrients directly through these leaf-like structures. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are clearly adaptations to dry land. For example, stomata are present on the stems of the sporophyte, and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate—whether it is soil, rock, or roof tiles—by multicellular **rhizoids**. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk. The moss lifecycle follows the pattern of alternation

of generations as shown in [\[link\]](#). The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a **protonema**—usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

Art Connection

This illustration shows the life cycle of mosses.
(credit: modification of work by Mariana Ruiz Villareal)



Which of the following statements about the moss life cycle is false?

1. The mature gametophyte is haploid.
2. The sporophyte produces haploid spores.
3. The calyptra buds to form a mature gametophyte.
4. The zygote is housed in the venter.

The slender **seta** (plural, setae), as seen in [\[link\]](#), contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the sporangium or **capsule**.



A structure called a **peristome** increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like “teeth”; these open and close depending on moisture levels, and periodically release spores.

Section Summary

Seedless nonvascular plants are small, having the gametophyte as the dominant stage of the lifecycle. Without a vascular system and roots, they absorb

water and nutrients on all their exposed surfaces. Collectively known as bryophytes, the three main groups include the liverworts, the hornworts, and the mosses. Liverworts are the most primitive plants and are closely related to the first land plants. Hornworts developed stomata and possess a single chloroplast per cell. Mosses have simple conductive cells and are attached to the substrate by rhizoids. They colonize harsh habitats and can regain moisture after drying out. The moss sporangium is a complex structure that allows release of spores away from the parent plant.

Art Connections

[\[link\]](#) Which of the following statements about the moss life cycle is false?

1. The mature gametophyte is haploid.
2. The sporophyte produces haploid spores.
3. The rhizoid buds to form a mature gametophyte.
4. The zygote is housed in the venter.

[\[link\]](#) C.

Review Questions

Which of the following structures is not found in bryophytes?

1. a cellulose cell wall
2. chloroplast
3. sporangium
4. root

D

Stomata appear in which group of plants?

1. Charales
2. liverworts
3. hornworts
4. mosses

C

The chromosome complement in a moss protonema is:

1. $1n$
2. $2n$
3. $3n$

4. varies with the size of the protonema

A

Why do mosses grow well in the Arctic tundra?

1. They grow better at cold temperatures.
 2. They do not require moisture.
 3. They do not have true roots and can grow on hard surfaces.
 4. There are no herbivores in the tundra.
-

C

Free Response

In areas where it rains often, mosses grow on roofs. How do mosses survive on roofs without soil?

Mosses absorb water and nutrients carried by the rain and do not need soil because they do not derive much nutrition from the soil.

What are the three classes of bryophytes?

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Glossary

capsule

case of the sporangium in mosses

gemma

(plural, gemmae) leaf fragment that spreads for asexual reproduction

hornworts

group of non-vascular plants in which stomata appear

liverworts

most primitive group of the non-vascular plants

mosses

group of bryophytes in which a primitive conductive system appears

peristome

tissue that surrounds the opening of the

capsule and allows periodic release of spores

protonema

tangle of single celled filaments that forms from the haploid spore

rhizoids

thin filaments that anchor the plant to the substrate

seta

stalk that supports the capsule in mosses

Seedless Plants

By the end of this section, you will be able to:

- Describe the distinguishing traits of the three types of bryophytes
- Identify the new traits that first appear in seedless vascular plants
- Describe the major classes of seedless vascular plants

An incredible variety of seedless plants populates the terrestrial landscape. Mosses grow on tree trunks, and horsetails ([\[link\]](#)) display their jointed stems and spindly leaves on the forest floor. Yet, seedless plants represent only a small fraction of the plants in our environment. Three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposing bodies created large deposits of coal that we mine today. Seedless plants like these horsetails (*Equisetum* sp.) thrive in damp, shaded environments under the tree canopy where dryness is a rare occurrence. (credit: Jerry Kirkhart)



Bryophytes

Bryophytes, an informal grouping of the nonvascular plants, are the closest extant relative of early terrestrial plants. The first bryophytes most probably appeared in the Ordovician period, about 490 million years ago. Because of the lack of lignin—the tough polymer in cell walls in the stems of vascular plants—and other resistant structures, the likelihood of bryophytes forming fossils is rather small, though some spores made up of sporopollenin have been discovered that have been attributed to early bryophytes. By the Silurian period (440 million years ago), however, vascular plants had spread throughout the continents. This fact is used as evidence that nonvascular plants must have preceded the Silurian period.

There are about 18,000 species of bryophytes, which thrive mostly in damp habitats, although some grow in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They do not have the specialized cells that conduct fluids found in the vascular plants, and generally lack lignin. In bryophytes, water and nutrients circulate inside specialized conducting cells. Although the name nontracheophyte is more accurate, bryophytes are commonly referred to as nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs belong to the haploid organism, or gametophyte. The diploid sporophyte is barely noticeable. The gametes formed by bryophytes swim using flagella. The sporangium, the multicellular sexual reproductive structure, is present in bryophytes. The embryo also remains attached to the parent plant, which nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three divisions (in plants, the taxonomic level “division” is used instead of phylum): the liverworts, or Marchantiophyta; the hornworts, or Anthocerotophyta; and the mosses, or true Bryophyta.

(a) A 1904 drawing of liverworts shows the variety of their forms. (b) A liverwort, *Lunularia cruciata*,

displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

Liverworts

Liverworts (Marchantiophyta) may be viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized many habitats on Earth and diversified to more than 6,000 existing species ([link](#)**a**). Some gametophytes form lobate green structures, as seen in [link](#)**b**. The shape is similar to the lobes of the liver and, hence, provides the origin of the common name given to the division.



(a)



(b)

Hornworts grow a tall and slender sporophyte.
(credit: modification of work by Jason Hollinger)

Hornworts

The **hornworts** (Anthocerotophyta) have colonized a variety of habitats on land, although they are never far from a source of moisture. There are about 100 described species of hornworts. The dominant phase of the life cycle of hornworts is the short, blue-green gametophyte. The sporophyte is the defining characteristic of the group. It is a long and narrow pipe-like structure that emerges from the parent gametophyte and maintains growth throughout the life of the plant ([\[link\]](#)).



This green feathery moss has reddish-brown sporophytes growing upward. (credit: "Lordgrunt"/Wikimedia Commons)

Mosses

More than 12,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, their shallow rhizoids allow them to fasten to a substrate without digging into the frozen soil. They slow down erosion, store moisture and soil nutrients, and provide shelter for small animals and food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor the quality of air. The sensitivity of mosses to copper salts makes these salts a common ingredient of compounds marketed to eliminate mosses in lawns ([\[link\]](#)).



Vascular Plants

The vascular plants are the dominant and most conspicuous group of land plants. There are about 275,000 species of vascular plants, which represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their spread to so many habitats.

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue are dated to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for long-distance transport of water and minerals, the transfer of water-soluble growth factors from the organs of synthesis to the target organs, and storage of water and nutrients.

A second type of vascular tissue is **phloem**, which transports sugars, proteins, and other solutes through the plant. Phloem cells are divided into sieve elements, or conducting cells, and supportive tissue. Together, xylem and phloem tissues form the vascular system of plants.

Roots: Support for the Plant

Roots are not well preserved in the fossil record; nevertheless, it seems that they did appear later in evolution than vascular tissue. The development of

an extensive network of roots represented a significant new feature of vascular plants. Thin rhizoids attached the bryophytes to the substrate. Their rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep in the ground to reach sources of water also stabilizes trees by acting as ballast and an anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae. In the mycorrhizae, fungal hyphae grow around the root and within the root around the cells, and in some instances within the cells. This benefits the plant by greatly increasing the surface area for absorption.

Leaves, Sporophylls, and Strobili

A third adaptation marks seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved photosynthetic efficiency. Leaves capture more sunlight with their increased surface area.

In addition to photosynthesis, leaves play another role in the life of the plants. Pinecones, mature fronds of ferns, and flowers are all **sporophylls**—leaves that were modified structurally to bear

sporangia. **Strobili** are structures that contain the sporangia. They are prominent in conifers and are known commonly as cones: for example, the pine cones of pine trees.

Lycopodium clavatum is a club moss. (credit: Cory Zanker) Horsetails thrive in a marsh. (credit: Myriam Feldman) Thin leaves originating at the joints are noticeable on the horsetail plant. (credit: Myriam Feldman) Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone) This chart shows the geological time scale, beginning with the Pre-Archean eon 3800 million years ago and ending with the Quaternary period in present time. (credit: modification of work by USGS) This campus garden was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

Seedless Vascular Plants

By the Late Devonian period (385 million years ago), plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period (359–299 million years ago), swamp forests of club mosses and horsetails, with some specimens reaching more than 30 meters tall, covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name. In seedless vascular plants, the sporophyte became the

dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless vascular plants include club mosses, horsetails, ferns, and whisk ferns.

Club Mosses

The **club mosses**, or Lycophyta, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous period, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and small leaves called microphylls ([\[link\]](#)). The division Lycophyta consists of close to 1,000 species, including quillworts (*Isoetales*), club mosses (Lycopodiales), and spike mosses (Selaginellales): none of which is a true moss.



Horsetails

Ferns and whisk ferns belong to the division Pterophyta. A third group of plants in the Pterophyta, the horsetails, is sometimes classified separately from ferns. **Horsetails** have a single genus, *Equisetum*. They are the survivors of a large group of plants, known as Arthrophyta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes ([\[link\]](#)).



The stem of a horsetail is characterized by the presence of joints, or nodes: hence the name *Arthrophyta*, which means “jointed plant”. Leaves and branches come out as whorls from the evenly spaced rings. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem ([\[link\]](#)).



Ferns and Whisk Ferns

Ferns are considered the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. Ferns form large leaves and branching roots. In contrast, **whisk ferns**, the psilophytes, lack both roots and leaves, which were probably lost by evolutionary reduction.

Evolutionary reduction is a process by which natural selection reduces the size of a structure that is no longer favorable in a particular environment.

Photosynthesis takes place in the green stem of a whisk fern. Small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns have been classified outside the true ferns; however, recent comparative analysis of DNA suggests that this group may have lost both vascular tissue and roots through evolution, and is actually closely related to ferns.

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants ([\[link\]](#)). About 12,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist and shaded places. They made their appearance in the fossil record during the Devonian period (416–359 million years ago) and expanded during the Carboniferous period, 359–299 million years ago ([\[link\]](#)).



EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	----- 1.6 -----
		Tertiary	----- 66 -----
	Mesozoic	Cretaceous	----- 138 -----
		Jurassic	----- 205 -----
		Triassic	----- 240 -----
	Paleozoic	Permian	----- 290 -----
		Carboniferous	----- 360 -----
		Devonian	----- 410 -----
		Silurian	----- 435 -----
		Ordovician	----- 500 -----
		Cambrian	----- 570 -----
Proterozoic			-----2500-----
Archean			-----3800?-----
Pre-Archean			

Concept in Action



Watch this [video](#) illustrating the life cycle of a fern and assess your knowledge.

Careers in Action

Landscape Designer

Looking at the well-laid gardens of flowers and fountains seen in royal castles and historic houses of Europe, it is clear that the creators of those gardens knew more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States' tradition. A prime example of early American classical design is Monticello, Thomas Jefferson's private estate; among his many other interests, Jefferson maintained a passion for botany. Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L'Enfant's design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens ([\[link\]](#)). The restoration of natural places encroached upon by human intervention, such as wetlands, also requires the expertise of a landscape designer. With such an array of required skills, a landscape designer's education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. For example, mosses and ferns will thrive in a shaded area where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of the individual plants must be taken into account to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.



Section Summary

Seedless nonvascular plants are small. The dominant stage of the life cycle is the gametophyte. Without a vascular system and roots, they absorb water and nutrients through all of their exposed surfaces. There are three main groups: the liverworts, the hornworts, and the mosses. They are collectively known as bryophytes.

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the vascular system, there appeared leaves—large photosynthetic organs—and roots to absorb water

from the ground. The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; horsetails, and ferns.

Multiple Choice

Why do mosses grow well in the Arctic tundra?

1. They grow better at cold temperatures.
2. They do not require moisture.
3. They do not have true roots and can grow on hard surfaces.
4. There are no herbivores in the tundra.

C

Which is the most diverse group of seedless vascular plants?

1. the liverworts
2. the horsetails
3. the club mosses
4. the ferns

D

Which group are vascular plants?

1. liverworts
2. mosses
3. hornworts
4. ferns

D

Free Response

What are the three classes of bryophytes?

The bryophytes are divided into three divisions: the liverworts or Marchantiophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

How did the development of a vascular system contribute to the increase in size of plants?

It became possible to transport water and nutrients through the plant and not be limited

by rates of diffusion. Vascularization allowed the development of leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Glossary

club moss

the earliest group of seedless vascular plants

fern

a seedless vascular plant that produces large fronds; the most advanced group of seedless vascular plants

hornwort

a group of non-vascular plants in which stomata appear

horsetail

a seedless vascular plant characterized by a jointed stem

liverwort

the most primitive group of non-vascular plants

moss

a group of plants in which a primitive conductive system appears

phloem

the vascular tissue responsible for transport of sugars, proteins, and other solutes

sporophyll

a leaf modified structurally to bear sporangia

strobili

cone-like structures that contain the sporangia

whisk fern

a seedless vascular plant that lost roots and leaves by evolutionary reduction

xylem

the vascular tissue responsible for long-distance transport of water and nutrients

Gymnosperms

By the end of this section, you will be able to:

- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- State which period saw the first appearance of gymnosperms and explain when they were the dominant plant life
- List the four groups of modern-day gymnosperms and provide examples of each

Gymnosperms, meaning “naked seeds,” are a diverse group of seed plants and are paraphyletic. Paraphyletic groups are those in which not all members are descendants of a single common ancestor. Their characteristics include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system).

Gymnosperm seeds are not enclosed in an ovary; rather, they are exposed on cones or modified leaves. Sporophylls are specialized leaves that produce sporangia. The term **strobilus** (plural = strobili) describes a tight arrangement of sporophylls around a central stalk, as seen in cones. Some seeds are enveloped by sporophyte tissues upon maturation. The layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo, is called the **integument**.

Gymnosperms were the dominant phylum in Mesozoic era. They are adapted to live where fresh water is scarce during part of the year, or in the nitrogen-poor soil of a bog. Therefore, they are still the prominent phylum in the coniferous biome or taiga, where the evergreen conifers have a selective advantage in cold and dry weather. Evergreen conifers continue low levels of photosynthesis during the cold months, and are ready to take advantage of the first sunny days of spring. One disadvantage is that conifers are more susceptible than deciduous trees to infestations because conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

The life cycle of a gymnosperm involves alternation of generations, with a dominant sporophyte in which the female gametophyte resides, and reduced gametophytes. All gymnosperms are heterosporous. The male and female reproductive organs can form in cones or strobili. Male and female sporangia are produced either on the same plant, described as **monoecious** (“one home” or bisexual), or on separate plants, referred to as **dioecious** (“two homes” or unisexual) plants. The life cycle of a conifer will serve as our example of reproduction in gymnosperms.

Life Cycle of a Conifer

Pine trees are conifers (cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous and generate two different types of spores: male microspores and female megaspores. In the male cones, or staminate cones, the **microsporocytes** give rise to pollen grains by meiosis. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube develops slowly, and the generative cell in the pollen grain divides into two haploid sperm cells by mitosis. At fertilization, one of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of a haploid egg cell.

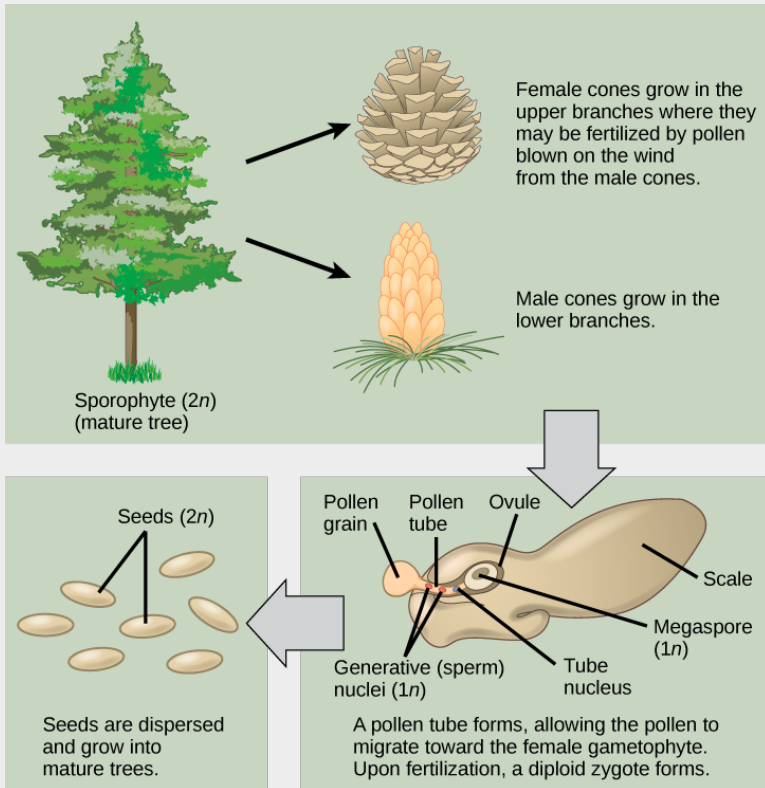
Female cones, or **ovulate cones**, contain two ovules per scale. One megaspore mother cell, or **megasporocyte**, undergoes meiosis in each ovule. Three of the four cells break down; only a single surviving cell will develop into a female multicellular gametophyte, which encloses archegonia (an archegonium is a reproductive organ that contains a single large egg). Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination. The seed that is formed contains

three generations of tissues: the seed coat that originates from the sporophyte tissue, the gametophyte that will provide nutrients, and the embryo itself.

[\[link\]](#) illustrates the life cycle of a conifer. The sporophyte ($2n$) phase is the longest phase in the life of a gymnosperm. The gametophytes ($1n$)—microspores and megaspores—are reduced in size. It may take more than year between pollination and fertilization while the pollen tube grows towards the megasporocyte ($2n$), which undergoes meiosis into megaspores. The megaspores will mature into eggs ($1n$).

Art Connection

This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.



At what stage does the diploid zygote form?

1. when the female cone begins to bud from the tree
2. at fertilization
3. when the seeds drop from the tree
4. when the pollen tube begins to grow

Link to Learning



Watch this video to see the process of seed production in gymnosperms.

<https://www.openstaxcollege.org/l/gymnosperm2>

Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce *Picea* sp., (b) juniper *Juniperus* sp., (c) sequoia *Sequoia Semervirens*, which is a deciduous gymnosperm, and (d) the tamarack *Larix larcinia*. Notice the yellow leaves of the tamarack. (credit a: modification of work by Rosendahl; credit b: modification of work by Alan Levine; credit c: modification of work by Wendy McCormic; credit d: modification of work by Micky Zlimen) This *Encephalartos ferox* cycad has large cones and broad, fern-like leaves. (credit: Wendy Cutler) This plate from the 1870 book *Flora Japonica, Sectio Prima (Tafelband)* depicts the leaves and fruit of *Ginkgo biloba*, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini. (a) *Ephedra viridis*, known by the common name *Mormon tea*, grows on the West Coast of the United States and Mexico. (b) *Gnetum gnemon* grows in

Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert. (credit a: modification of work by USDA; credit b: modification of work by Malcolm Manners; credit c: modification of work by Derek Keats)

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. Coniferophyta, Cycadophyta, and Ginkgophyta are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, the three phyla are not closely related phylogenetically to each other. Gnetophyta are considered the closest group to angiosperms because they produce true xylem tissue.

Conifers (Coniferophyta)

Conifers are the dominant phylum of gymnosperms, with the most variety of species ([\[link\]](#)). Most are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to cold and dry weather explain the

predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous and lose their leaves in fall. The European larch and the tamarack are examples of deciduous conifers ([link]c). Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is therefore referred to as “soft wood.”



(a)



(b)



(c)



(d)

Cycads

Cycads thrive in mild climates, and are often mistaken for palms because of the shape of their large, compound leaves. Cycads bear large cones ([\[link\]](#)), and may be pollinated by beetles rather than wind: unusual for a gymnosperm. They dominated the landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. They face possible extinction, and several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens in the tropics and subtropics.



Gingkophytes

The single surviving species of the **gingkophytes** group is the *Ginkgo biloba* ([\[link\]](#)). Its fan-shaped

leaves—unique among seed plants because they feature a dichotomous venation pattern—turn yellow in autumn and fall from the tree. For centuries, *G. biloba* was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.



Gnetophytes

Gnetophytes are the closest relative to modern angiosperms, and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia* ([\[link\]](#)). Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of

the West Coast of the United States and Mexico. *Ephedra*'s small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.



(a) *Ephedra*



(b) *Gnetum*



(c) *Welwitschia*

Link to Learning



Watch this BBC video describing the amazing strangeness of Welwitschia.

<https://www.openstaxcollege.org/l/welwitschia2>

Section Summary

Gymnosperms are heterosporous seed plants that produce naked seeds. They appeared in the Paleozoic period and were the dominant plant life during the Mesozoic. Modern-day gymnosperms belong to four phyla. The largest phylum, Coniferophyta, is represented by conifers, the predominant plants at high altitude and latitude. Cycads (phylum Cycadophyta) resemble palm trees and grow in tropical climates. *Ginkgo biloba* is the only representative of the phylum Ginkgophyta. The last phylum, Gnetophyta, is a diverse group of shrubs that produce vessel elements in their wood.

Art Connections

[\[link\]](#) At what stage does the diploid zygote form?

1. When the female cone begins to bud from the tree
2. At fertilization
3. When the seeds drop from the tree
4. When the pollen tube begins to grow

[\[link\]](#) B. The diploid zygote forms after the pollen tube has finished forming, so that the male generative nuclei can fuse with the female gametophyte.

Review Questions

Which of the following traits characterizes gymnosperms?

1. The plants carry exposed seeds on modified leaves.
2. Reproductive structures are located in a flower.
3. After fertilization, the ovary thickens and forms a fruit.
4. The gametophyte is longest phase of the life cycle.

A

Megasporocytes will eventually produce which of the following?

1. pollen grain
2. sporophytes

3. male gametophytes
 4. female gametophytes
-

D

What is the ploidy of the following structures:
gametophyte, seed, spore, sporophyte?

1. $1n$, $1n$, $2n$, $2n$
 2. $1n$, $2n$, $1n$, $2n$
 3. $2n$, $1n$, $2n$, $1n$
 4. $2n$, $2n$, $1n$, $1n$
-

B

In the northern forests of Siberia, a tall tree is
most likely a:

1. conifer
 2. cycad
 3. *Ginkgo biloba*
 4. gnetophyte
-

A

Free Response

The Mediterranean landscape along the sea shore is dotted with pines and cypresses. The weather is not cold, and the trees grow at sea level. What evolutionary adaptation of conifers makes them suitable to the Mediterranean climate?

The trees are adapted to arid weather, and do not lose as much water due to transpiration as non-conifers.

What are the four modern-day phyla of gymnosperms?

The four modern-day phyla of gymnosperms are Coniferophyta, Cycadophyta, Ginkgophyta, and Gnetophyta.

Glossary

conifer

dominant phylum of gymnosperms with the most variety of trees

cycad

gymnosperm that grows in tropical climates and resembles a palm tree; member of the phylum Cycadophyta

dioecious

describes a species in which the male and female reproductive organs are carried on separate specimens

gingkophyte

gymnosperm with one extant species, the *Ginkgo biloba*: a tree with fan-shaped leaves

gnetophyte

gymnosperm shrub with varied morphological features that produces vessel elements in its woody tissues; the phylum includes the genera *Ephedra*, *Gnetum* and *Welwitschia*

gymnosperm

seed plant with naked seeds (seeds exposed on modified leaves or in cones)

integument

layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo

megasporocyte

megaspore mother cell; larger spore that germinates into a female gametophyte in a heterosporous plant

microsporocyte

smaller spore that produces a male gametophyte in a heterosporous plant

monoecious

describes a species in which the male and female reproductive organs are on the same plant

ovulate cone

cone containing two ovules per scale

strobilus

plant structure with a tight arrangement of sporophylls around a central stalk, as seen in cones or flowers; the male strobilus produces pollen, and the female strobilus produces eggs

Angiosperms

By the end of this section, you will be able to:

- Explain why angiosperms are the dominant form of plant life in most terrestrial ecosystems
- Describe the main parts of a flower and their purpose
- Detail the life cycle of an angiosperm
- Discuss the two main groups of flowering plants

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems ([\[link\]](#)). With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification.

These flowers grow in a botanical garden border in Bellevue, WA. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by animals such as insects and birds. (credit: Myriam Feldman)



The success of angiosperms is due to two novel reproductive structures: flowers and fruit. The function of the flower is to ensure pollination. Flowers also provide protection for the ovule and developing embryo inside a receptacle. The function of the fruit is seed dispersal. They also protect the developing seed. Different fruit structures or tissues on fruit—such as sweet flesh, wings, parachutes, or spines that grab—reflect the dispersal strategies that help spread seeds.

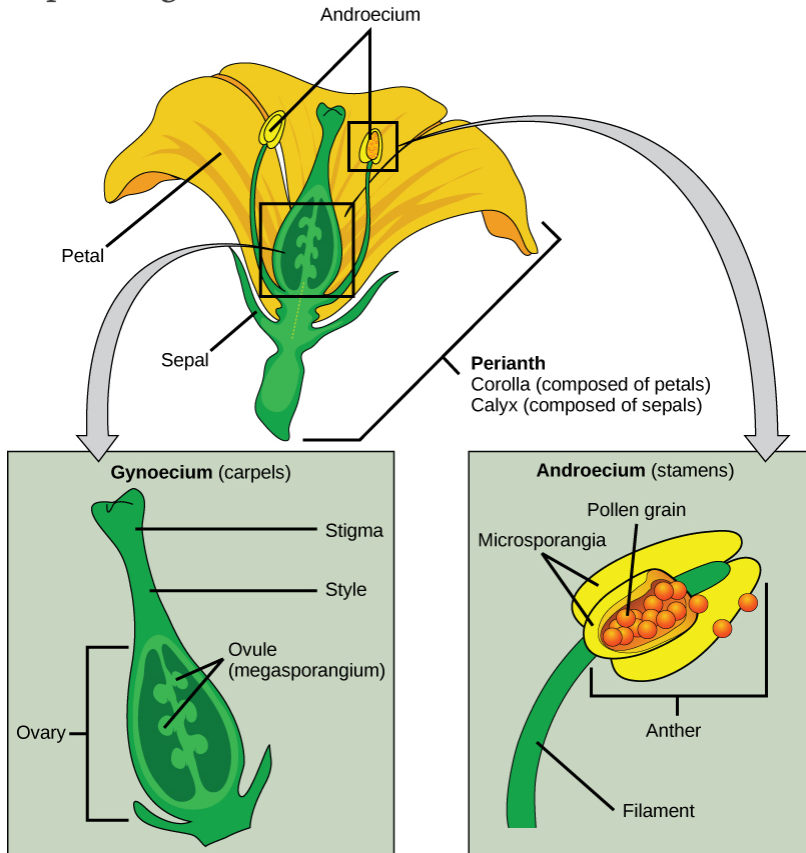
This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium. (credit: modification of work by Mariana Ruiz Villareal)

Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens. The peduncle attaches the flower to the plant. A whorl of **sepals** (collectively called the **calyx**) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. **Petals**, collectively the **corolla**, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the **perianth**. The sexual organs (carpels and stamens) are located at the center of the flower.

As illustrated in [\[link\]](#), styles, stigmas, and ovules constitute the female organ: the **gynoecium** or **carpel**. Flower structure is very diverse, and carpels may be singular, multiple, or fused. Multiple fused carpels comprise a **pistil**. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a **style** leads from the sticky **stigma**, where pollen is deposited, to the **ovary**, enclosed in the

carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the **stamens** (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a **filament** and a sac-like structure called the anther. The filament supports the **anther**, where the microspores are produced by meiosis and develop into pollen grains.



Fruit

As the seed develops, the walls of the ovary thicken and form the fruit. The seed forms in an ovary, which also enlarges as the seeds grow. In botany, a fertilized and fully grown, ripened ovary is a fruit. Many foods commonly called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns are nuts, and winged maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle and apples from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and orange, have rinds. Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten,

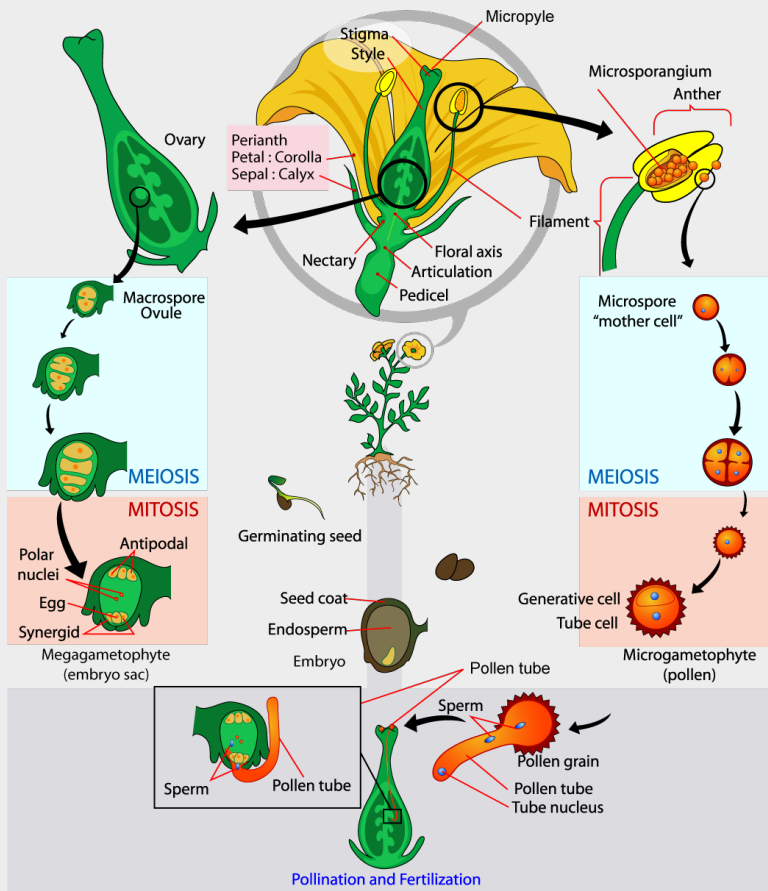
tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle ([\[link\]](#)). Like gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will generate pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

Art Connection

The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)



If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes

meiosis, generating four megaspores—three small and one large. Only the large megaspore survives; it produces the female gametophyte, referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator, and will eventually fuse to form a $2n$ polar nucleus; the three cells away from the egg form antipodals, and the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids or “helper” cells, three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle: an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote—the future embryo. The other sperm fuses with the $2n$ polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called **cotyledons**. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are

stored outside the embryo, in the form of complex carbohydrates, lipids or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and at the center, the well-protected embryo.

Most flowers are monoecious or bisexual, which means that they carry both stamens and carpels; only a few species self-pollinate. Monoecious flowers are also known as “perfect” flowers because they contain both types of sex organs ([\[link\]](#)). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water), or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

The (a) common spicebush belongs to the *Laurales*, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrum* plant is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since ancient times for their ornamental value; the root of the lotus flower is eaten as a vegetable. The red seeds of (d) a magnolia tree, characteristic of the final stage, are just starting to appear. (credit a: modification of work by Cory Zanker; credit b: modification of work by Franz

Eugen Köhler; credit c: modification of work by "berduchwal"/Flickr; credit d: modification of work by "Coastside2"/Wikimedia Commons). The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots. (credit a: modification of work by David Nance, USDA ARS; credit b, c: modification of work by Rosendahl; credit d: modification of work by Bill Tarpenning, USDA; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Keith Weller, USDA)

Diversity of Angiosperms

Angiosperms are classified in a single phylum: the **Anthophyta**. Modern angiosperms appear to be a monophyletic group, which means that they originate from a single ancestor. Flowering plants are divided into two major groups, according to the structure of the cotyledons, pollen grains, and other structures. **Monocots** include grasses and lilies, and eudicots or **dicots** form a polyphyletic group. **Basal angiosperms** are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes. The *Magnoliidae* (magnolia trees, laurels, and water lilies) and the *Piperaceae* (peppers) belong to the basal angiosperm group.

Basal Angiosperms

The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic ([\[link\]](#)d). Laurel trees produce fragrant leaves and small, inconspicuous flowers. The *Laurales* grow mostly in warmer climates and are small trees and shrubs. Familiar plants in this group include the bay laurel, cinnamon, spice bush ([\[link\]](#)a), and avocado tree. The *Nymphaeales* are comprised of the water lilies, lotus ([\[link\]](#)c), and similar plants; all species thrive in freshwater biomes, and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners, and have graced ponds and pools for thousands of years. The *Piperales* are a group of herbs, shrubs, and small trees that grow in the tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many species are the source of prized fragrance or spices, for example the berries of *Piper nigrum* ([\[link\]](#)b) are the familiar black peppercorns that are used to flavor many dishes.



(a)



(b)



(c)



(d)

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves, and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm

trees, vascular and parenchyma tissues produced by the primary and secondary thickening meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are at the origin of their alternate name of Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples ([\[link\]](#)).

Monocots



(a) Rice



(b) Wheat



(c) Bananas

Dicots



(d) Cabbage



(e) Beans



(f) Peaches

Eudicots

Eudicots, or true dicots, are characterized by the

presence of two cotyledons in the developing shoot. Veins form a network in leaves, and flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem; in monocots, vascular tissue is scattered in the stem. Eudicots can be **herbaceous** (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants. The major differences between monocots and eudicots are summarized in [\[link\]](#). Many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a eudicot is not always clearly evident.

**Comparison of
Structural
Characteristics
of Monocots
and Eudicots**

Characteristic	Monocot	Eudicot
Cotyledon	One	Two
Veins in Leaves	Parallel	Network (branched)
Stem Vascular	Scattered	Arranged in ring

Tissue			pattern
Roots	Network of adventitious roots		Tap root with many lateral roots
Pollen	Monosulcate		Trisulcate
Flower Parts	Three or multiple of three	Four, five, multiple of four or five and whorls	

Section Summary

Angiosperms are the dominant form of plant life in most terrestrial ecosystems, comprising about 90 percent of all plant species. Most crops and ornamental plants are angiosperms. Their success comes from two innovative structures that protect reproduction from variability in the environment: the flower and the fruit. Flowers were derived from modified leaves. The main parts of a flower are the sepals and petals, which protect the reproductive parts: the stamens and the carpels. The stamens produce the male gametes in pollen grains. The carpels contain the female gametes (the eggs inside the ovules), which are within the ovary of a carpel. The walls of the ovary thicken after fertilization, ripening into fruit that ensures dispersal by wind, water, or animals.

The angiosperm life cycle is dominated by the sporophyte stage. Double fertilization is an event unique to angiosperms. One sperm in the pollen fertilizes the egg, forming a diploid zygote, while the other combines with the two polar nuclei, forming a triploid cell that develops into a food storage tissue called the endosperm. Flowering plants are divided into two main groups, the monocots and eudicots, according to the number of cotyledons in the seedlings. Basal angiosperms belong to an older lineage than monocots and eudicots.

Art Connections

[\[link\]](#) If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

[\[link\]](#) Without a megasporangium, an egg would not form; without a microsporangium, pollen would not form.

Review Questions

Which of the following structures in a flower is not directly involved in reproduction?

1. the style
2. the stamen
3. the sepal
4. the anther

C

Pollen grains develop in which structure?

1. the anther
2. the stigma
3. the filament
4. the carpel

A

In the course of double fertilization, one sperm cell fuses with the egg and the second one fuses with _____.

1. the synergids
 2. the polar nuclei of the center cell
 3. the egg as well
 4. the antipodal cells
-

B

Corn develops from a seedling with a single cotyledon, displays parallel veins on its leaves, and produces monosulcate pollen. It is most likely:

1. a gymnosperm
2. a monocot
3. a eudicot
4. a basal angiosperm

B

Free Response

Some cycads are considered endangered species and their trade is severely restricted. Customs officials stop suspected smugglers who claim that the plants in their possession are palm trees, not cycads. How would a botanist distinguish between the two types of plants?

The resemblance between cycads and palm trees is only superficial. Cycads are

gymnosperms and do not bear flowers or fruit. Cycads produce cones: large, female cones that produce naked seeds, and smaller male cones on separate plants. Palms do not.

What are the two structures that allow angiosperms to be the dominant form of plant life in most terrestrial ecosystems?

Angiosperms are successful because of flowers and fruit. These structures protect reproduction from variability in the environment.

Glossary

anther

sac-like structure at the tip of the stamen in which pollen grains are produced

Anthophyta

phylum to which angiosperms belong

basal angiosperms

a group of plants that probably branched off before the separation of monocots and eudicots

calyx

whorl of sepals

carpel
single unit of the pistil

corolla
collection of petals

cotyledon
primitive leaf that develop in the zygote;
monocots have one cotyledon, and dicots
have two cotyledons

dicot
(also, eudicot) related group of angiosperms
whose embryos possess two cotyledons

filament
thin stalk that links the anther to the base of
the flower

gynoecium
(also, carpel) structure that constitute the
female reproductive organ

herbaceous
grass-like plant noticeable by the absence of
woody tissue

monocot
related group of angiosperms that produce
embryos with one cotyledon and pollen with
a single ridge

ovary

chamber that contains and protects the ovule
or female megasporangium

perianth

part of the plant consisting of the calyx
(sepals) and corolla (petals)

petal

modified leaf interior to the sepals; colorful
petals attract animal pollinators

pistil

fused group of carpels

sepal

modified leaf that encloses the bud;
outermost structure of a flower

stamen

structure that contains the male reproductive
organs

stigma

uppermost structure of the carpel where
pollen is deposited

style

long, thin structure that links the stigma to
the ovary

Features Used to Classify Animals

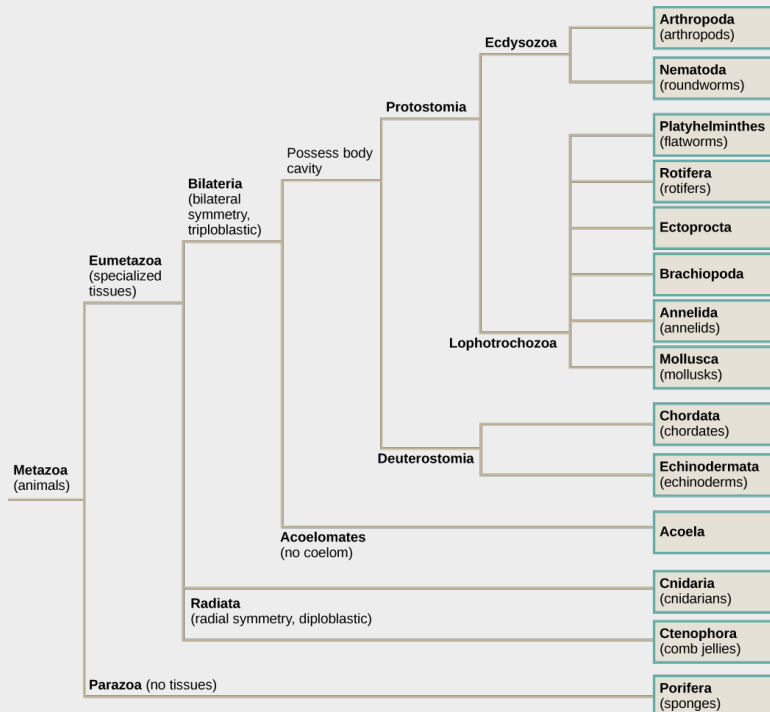
By the end of this section, you will be able to:

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most “rules” governing animal classification ([\[link\]](#)). Animals are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

Art Connection

The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.



Which of the following statements is false?

1. Eumetazoans have specialized tissues and parazoans don't.
2. Lophotrochozoa and Ecdysozoa are both Bilateria.
3. Acoela and Cnidaria both possess radial symmetry.
4. Arthropods are more closely related to nematodes than they are to annelids.

The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d)

butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)The bilaterally symmetrical human body can be divided into planes.

Animal Characterization Based on Body Symmetry

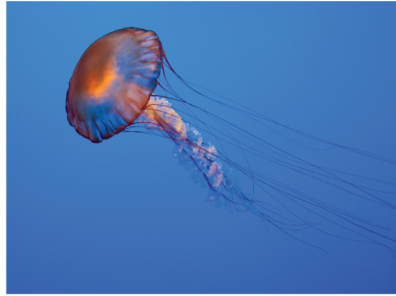
At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa ([link](#)a). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or “oral side,” and the side without a mouth (the “aboral side”). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones

([\[link\]](#)bc). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.



(a)



(b)



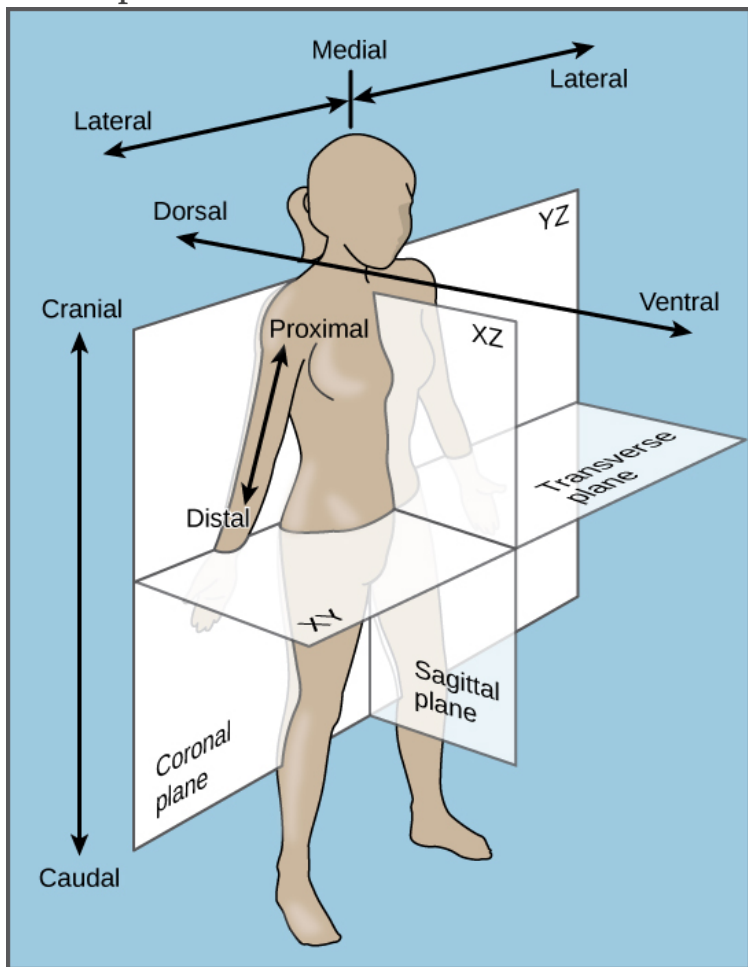
(c)



(d)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly ([\[link\]](#)d), crab, or human body. Animals with bilateral symmetry have a “head” and “tail” (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides ([\[link\]](#)). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a

phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal's anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.



Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Link to Learning



Watch this video to see a quick sketch of the different types of body symmetry.

<https://www.openstaxcollege.org/l/symmetry>

Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates.

Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm.

Pseudocoelomates also have a body cavity, but it is

sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS) Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

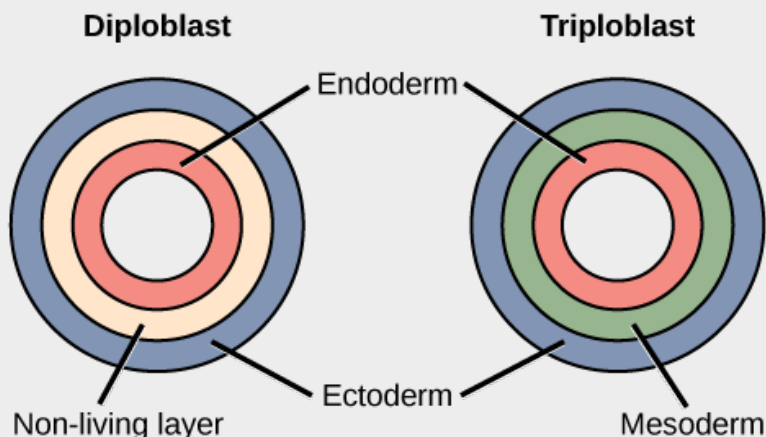
Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals develop either two or three embryonic germ layers ([\[link\]](#)). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called **diploblasts**. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer

(ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called **triploblasts**.

Art Connection

During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.



Which of the following statements about diploblasts and triploblasts is false?

1. Animals that display radial symmetry are diploblasts.
2. Animals that display bilateral symmetry are triploblasts.
3. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
4. The mesoderm gives rise to the central

nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. The endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal body cavity derived from mesoderm, called a **coelom**, and those that do not. This epithelial cell-lined coelomic cavity represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system,

kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. Organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called **acoelomates**, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called **eucoelomates** (or coelomates) ([\[link\]](#)). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is

found between the two layers. Although still functional, these are considered false coeloms, and those animals are called **pseudocoelomates**. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.



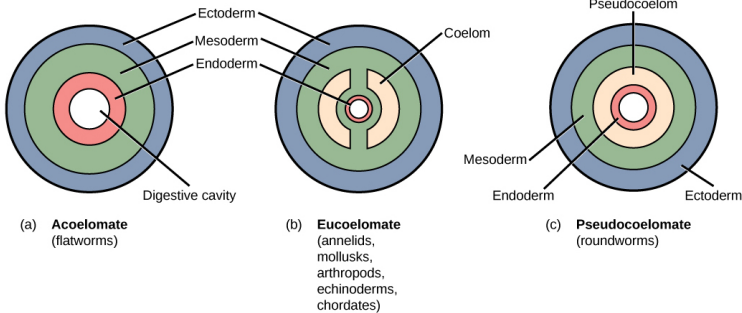
Flatworm: *Pseudobiceros bedfordi*



Annelid: *Glycera*



Nematode: *Heterodera glycines*



Embryonic Development of the Mouth

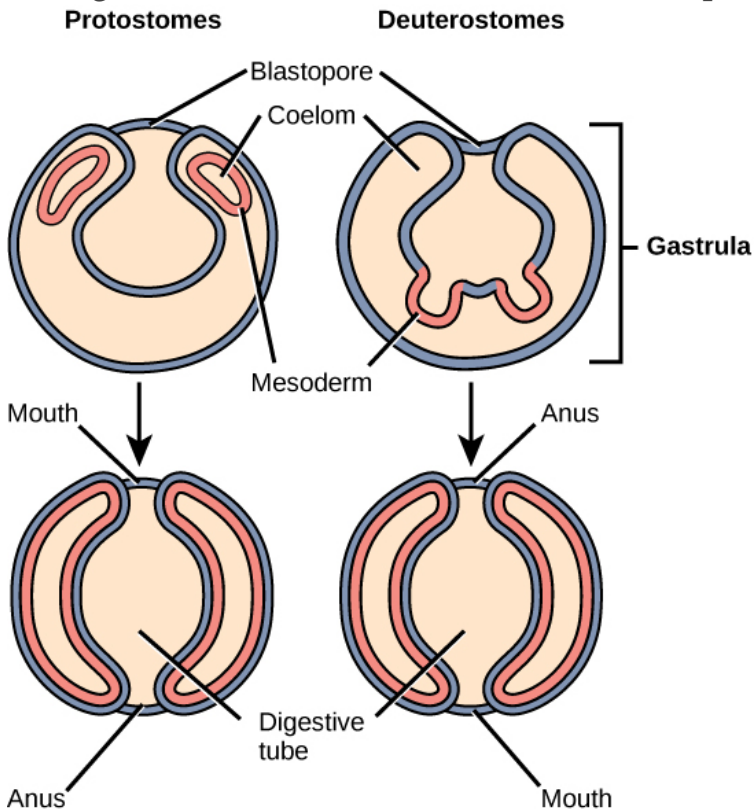
Bilaterally symmetrical, triploblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. **Protostomes** include arthropods, mollusks, and annelids. **Deuterostomes** include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word

protostome comes from the Greek word meaning “mouth first,” and deuterostome originates from the word meaning “mouth second” (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore ([\[link\]](#)). The **blastopore** is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus ([\[link\]](#)). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called **schizocoely**, meaning that during development, a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called **enterocoely**. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and

deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo **spiral cleavage**, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo **radial cleavage**, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.



There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also

undergo **determinate cleavage**. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo **indeterminate cleavage**, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Evolution Connection

The Evolution of the Coelom

One of the first steps in the classification of animals is to examine the animal's body. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such

as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.

Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.

Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have evolved from coelomates and may have lost their ability to form a coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

Section Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

Art Connections

[\[link\]](#) Which of the following statements is false?

1. Eumetazoans have specialized tissues and parazoans don't.
 2. Lophotrochozoa and Ecdysozoa are both Bilateria.
 3. Acoela and Cnidaria both possess radial symmetry.
 4. Arthropods are more closely related to nematodes than they are to annelids.
-

[\[link\]](#) C

[\[link\]](#) Which of the following statements about diploblasts and triploblasts is false?

1. Animals that display radial symmetry are diploblasts.
 2. Animals that display bilateral symmetry are triploblasts.
 3. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
 4. The mesoderm gives rise to the central nervous system.
-

[\[link\]](#) D

Review Questions

Which of the following organism is most likely to be a diploblast?

1. sea star
2. shrimp
3. jellyfish
4. insect

C

Which of the following is not possible?

1. radially symmetrical diploblast
2. diploblastic eucoelomate
3. protostomic coelomate
4. bilaterally symmetrical deuterostome

B

An animal whose development is marked by radial cleavage and enterocoely is _____.

1. a deuterostome
2. an annelid or mollusk
3. either an acoelomate or eucoelomate
4. none of the above

Free Response

Using the following terms, explain what classifications and groups humans fall into, from the most general to the most specific: symmetry, germ layers, coelom, cleavage, embryological development.

Humans have body plans that are bilaterally symmetrical and are characterized by the development of three germ layers, making them triploblasts. Humans have true coeloms and are thus eucoelomates. As deuterostomes, humans are characterized by radial and indeterminate cleavage.

Explain some of the advantages brought about through the evolution of bilateral symmetry and coelom formation.

The evolution of bilateral symmetry led to designated head and tail body regions, and promoted more efficient mobility for animals.

This improved mobility allowed for more skillful seeking of resources and prey escaping from predators. The appearance of the coelom in coelomates provides many internal organs with shock absorption, making them less prone to physical damage from bodily assault. A coelom also gives the body greater flexibility, which promotes more efficient movement. The relatively loose placement of organs within the coelom allows them to develop and grow with some spatial freedom, which promoted the evolution of optimal organ arrangement. The coelom also provides space for a circulatory system, which is an advantageous way to distribute body fluids and gases.

Glossary

acoelomate

animal without a body cavity

bilateral symmetry

type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore

indentation formed during gastrulation, evident in the gastrula stage

coelom

lined body cavity

determinate cleavage

developmental tissue fate of each embryonic cell is already determined

deuterostome

blastopore develops into the anus, with the second opening developing into the mouth

diploblast

animal that develops from two germ layers

enterocoely

mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate

animal with a body cavity completely lined with mesodermal tissue

indeterminate cleavage

early stage of development when germ cells or “stem cells” are not yet pre-determined to develop into specific cell types

protostome

blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate

animal with a body cavity located between the mesoderm and endoderm

radial cleavage

cleavage axes are parallel or perpendicular to the polar axis, resulting in the alignment of cells between the two poles

radial symmetry

type of symmetry with multiple planes of symmetry, with body parts (rays) arranged around a central disk

schizocoely

during development of protostomes, a solid mass of mesoderm splits apart and forms the hollow opening of the coelom

spiral cleavage

cells of one pole of the embryo are rotated or misaligned with respect to the cells of the opposite pole

triploblast

animal that develops from three germ layers

Digestive Systems

By the end of this section, you will be able to:

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman) Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects

called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan) Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in [\[link\]](#) include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



(a)



(b)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in [\[link\]](#)**a** and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in [\[link\]](#)**b**. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a)



(b)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in [\[link\]a](#)), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in [\[link\]b](#)).



(a)



(b)

(a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

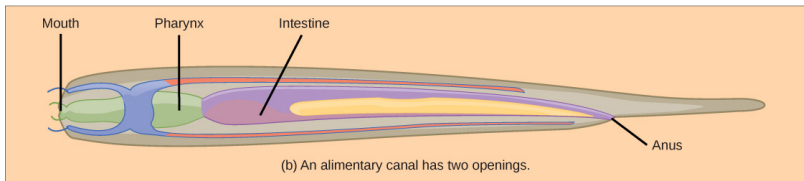
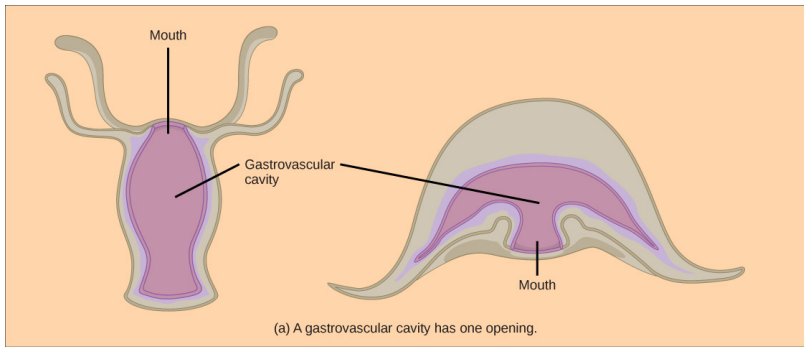
Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a **gastrovascular cavity** and is found in organisms with only one opening for digestion.

Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in [\[link\]](#)a, are typically a blind tube or cavity with only one opening, the “mouth”, which also serves as an “anus”. Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The **alimentary canal**, shown in [\[link\]](#)b, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other.

Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.



(a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them. The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine

and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca. Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

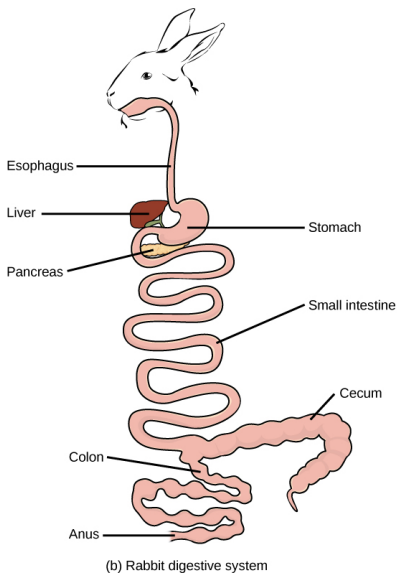
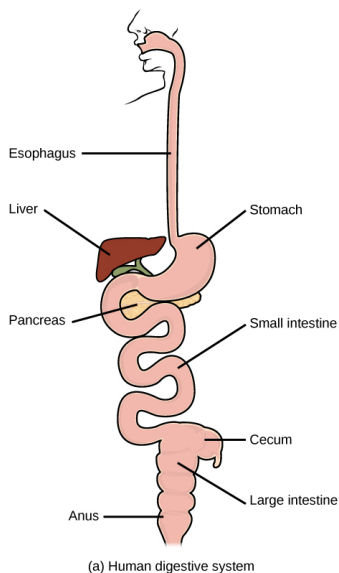
Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word **monogastric** suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system as illustrated in [\[link\]](#)**ab**. The process of digestion begins with the

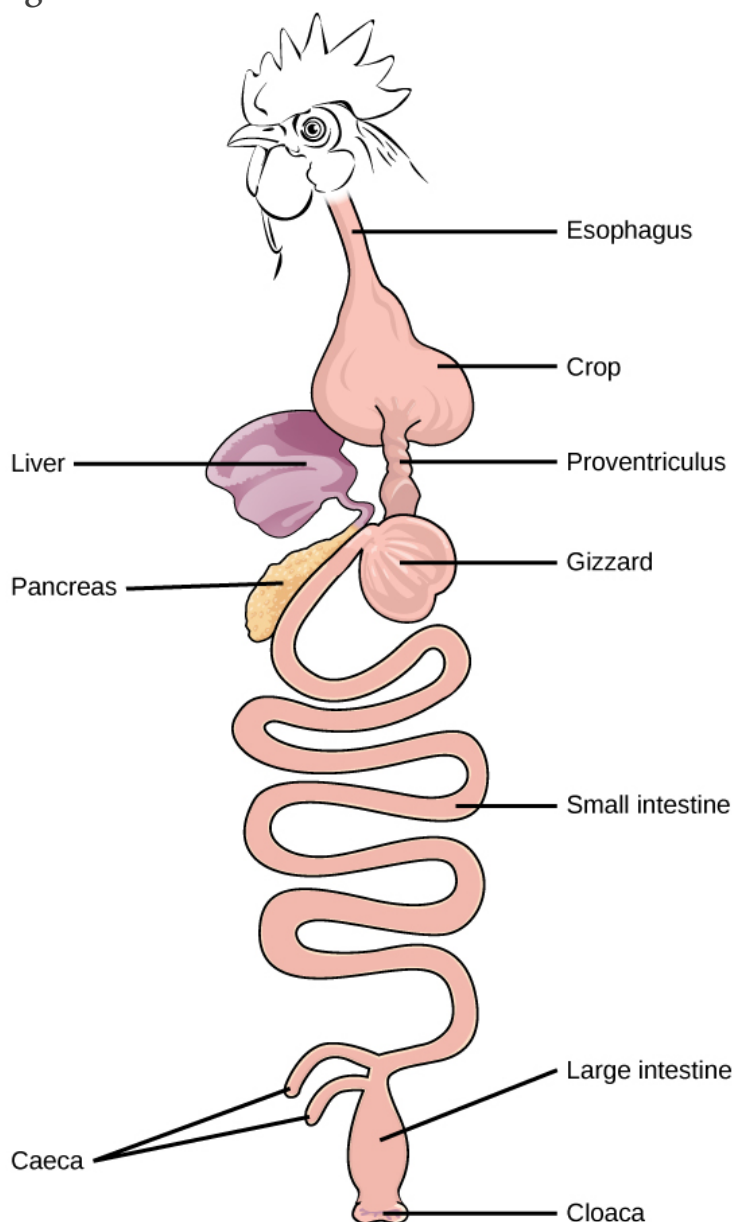
mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.



Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in [\[link\]](#), must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the **proventriculus**, where gastric juices are produced to digest the food before it enters the stomach, and the **gizzard**, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated.

Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.



Evolution Connection

Avian Adaptations

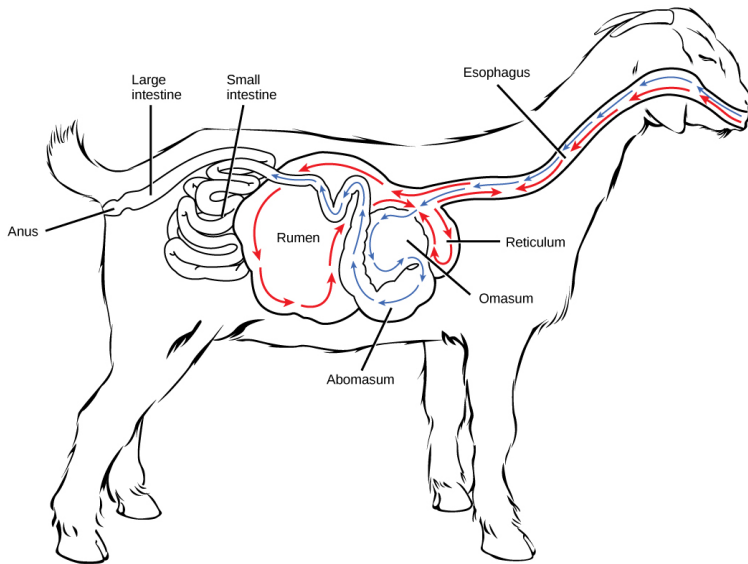
Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of **roughage** or fiber. They have evolved digestive systems that help them digest vast

amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in [\[link\]](#). The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the “true” stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.



Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the

roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute) The esophagus transfers food from the mouth to the stomach through peristaltic movements. The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Parts of the Digestive System

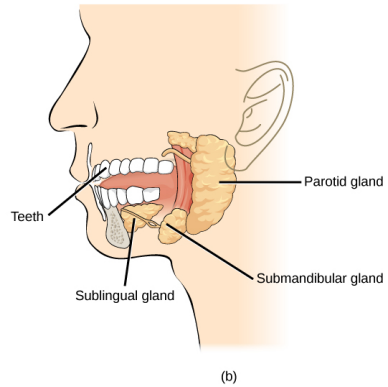
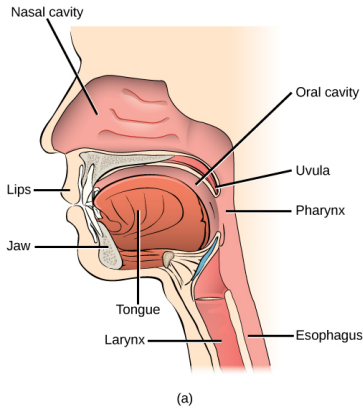
The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in [\[link\]](#). The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

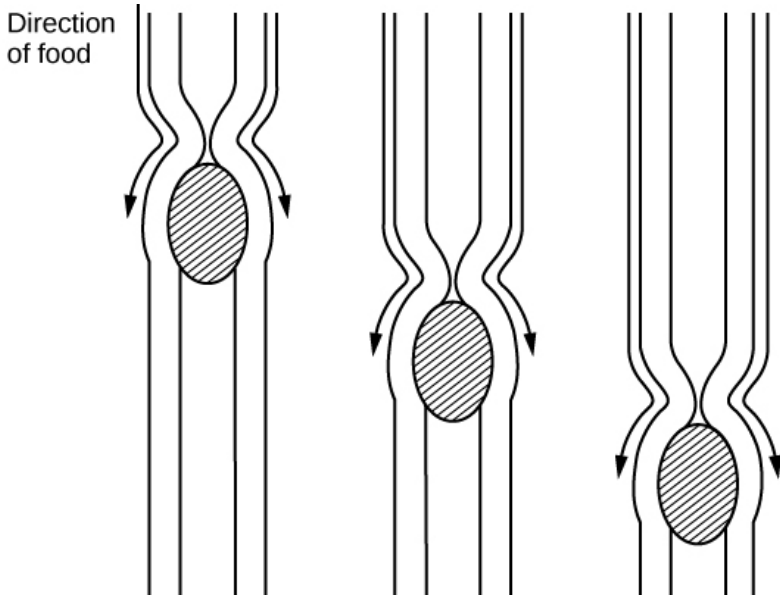
The extensive chemical process of digestion begins

in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called **salivary amylase** that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called **lipase** is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the **bolus** for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.



Esophagus

The **esophagus** is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called **peristalsis** that push the food toward the stomach, as illustrated in [\[link\]](#). The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.



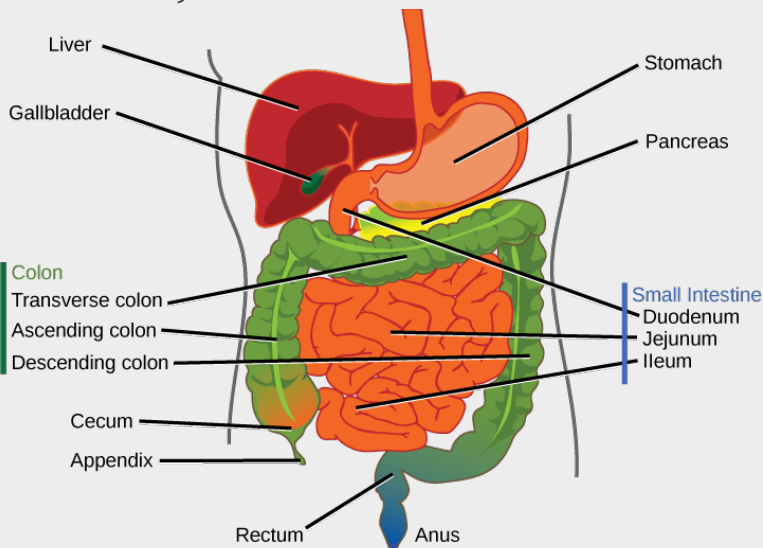
A ring-like muscle called a **sphincter** forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or “heartburn” occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in [\[link\]](#). The **stomach** is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Art Connection

The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)



Which of the following statements about the

digestive system is false?

1. Chyme is a mixture of food and digestive juices that is produced in the stomach.
2. Food enters the large intestine before the small intestine.
3. In the small intestine, chyme mixes with bile, which emulsifies fats.
4. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. **Pepsin** is secreted by the chief cells in the stomach in an inactive form called **pepsinogen**. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion

is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called **chyme**. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

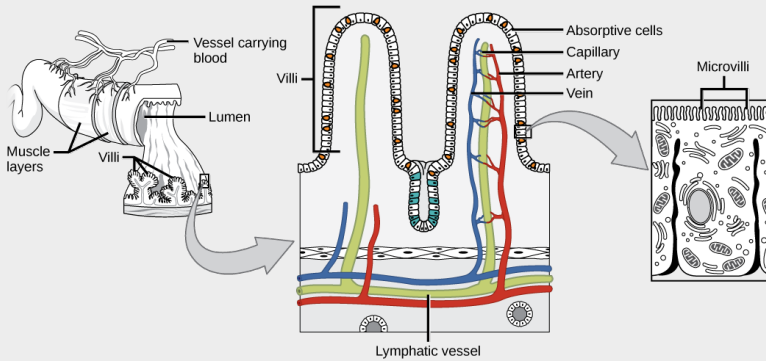
When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the **villi**. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in [\[link\]](#), are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Art Connection

Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.



Which of the following statements about the small intestine is false?

1. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
2. The inside of the small intestine has many folds, called villi.
3. Microvilli are lined with blood vessels as well as lymphatic vessels.
4. The inside of the small intestine is called the lumen.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The “C-shaped,” fixed part of the small intestine is called the **duodenum** and is shown in [\[link\]](#). The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with

pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. **Bile** is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

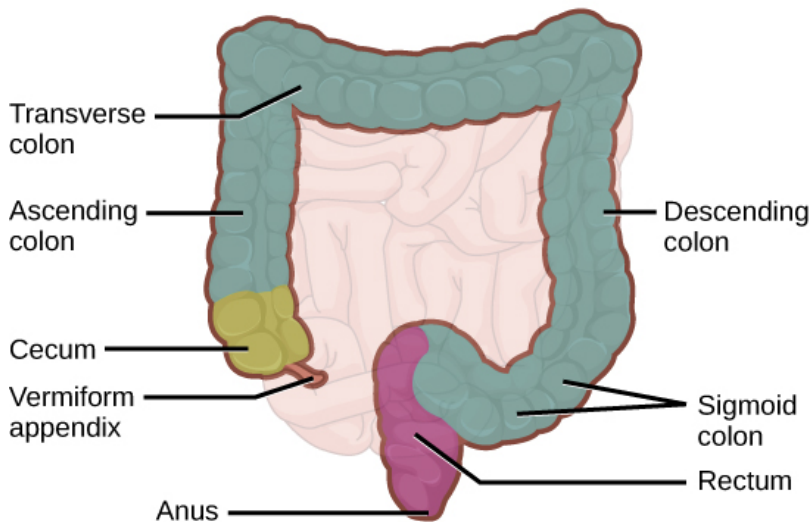
The second part of the small intestine is called the **jejunum**, shown in [\[link\]](#). Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The **ileum**, also illustrated in [\[link\]](#) is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal

valve. The vermiform, “worm-like,” appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The **large intestine**, illustrated in [\[link\]](#), reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or “intestinal flora” that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.



Rectum and Anus

The **rectum** is the terminal end of the large intestine, as shown in [\[link\]](#). The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that

catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The **liver** is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The **pancreas** is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The **gallbladder** is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Section Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Art Connections

[\[link\]](#) Which of the following statements about the digestive system is false?

1. Chyme is a mixture of food and digestive juices that is produced in the stomach.
 2. Food enters the large intestine before the small intestine.
 3. In the small intestine, chyme mixes with bile, which emulsifies fats.
 4. The stomach is separated from the small intestine by the pyloric sphincter.
-

[\[link\]](#) B

[\[link\]](#) Which of the following statements about the small intestine is false?

1. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
2. The inside of the small intestine has many folds, called villi.
3. Microvilli are lined with blood vessels as

well as lymphatic vessels.

4. The inside of the small intestine is called the lumen.

[\[link\]](#) C

Review Questions

Which of the following is a pseudo-ruminant?

1. cow
2. pig
3. crow
4. horse

D

Which of the following statements is untrue?

1. Roughage takes a long time to digest.
2. Birds eat large quantities at one time so that they can fly long distances.
3. Cows do not have upper teeth.
4. In pseudo-ruminants, roughage is digested in the cecum.

B

The acidic nature of chyme is neutralized by _____.

1. potassium hydroxide
2. sodium hydroxide
3. bicarbonates
4. vinegar

C

The digestive juices from the liver are delivered to the _____.

1. stomach
2. liver
3. duodenum
4. colon

C

Free Response

How does the polygastric digestive system aid in digesting roughage?

Animals with a polygastric digestive system have a multi-chambered stomach. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down the cellulose and ferment the ingested food. The abomasum is the “true” stomach and is the equivalent of a monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary for ruminants to digest plant material.

How do birds digest their food in the absence of teeth?

Birds have a stomach chamber called a gizzard. Here, the food is stored, soaked, and ground into finer particles, often using pebbles. Once this process is complete, the digestive juices take over in the proventriculus and continue the digestive process.

What is the role of the accessory organs in

digestion?

Accessory organs play an important role in producing and delivering digestive juices to the intestine during digestion and absorption. Specifically, the salivary glands, liver, pancreas, and gallbladder play important roles. Malfunction of any of these organs can lead to disease states.

Explain how the villi and microvilli aid in absorption.

The villi and microvilli are folds on the surface of the small intestine. These folds increase the surface area of the intestine and provide more area for the absorption of nutrients.

Glossary

alimentary canal

tubular digestive system with a mouth and anus

anus

exit point for waste material

bile

digestive juice produced by the liver;
important for digestion of lipids

bolus

mass of food resulting from chewing action
and wetting by saliva

carnivore

animal that consumes animal flesh

chyme

mixture of partially digested food and
stomach juices

duodenum

first part of the small intestine where a large
part of digestion of carbohydrates and fats
occurs

esophagus

tubular organ that connects the mouth to the
stomach

gallbladder

organ that stores and concentrates bile

gastrovascular cavity

digestive system consisting of a single
opening

gizzard

muscular organ that grinds food

herbivore

animal that consumes strictly plant diet

ileum

last part of the small intestine; connects the small intestine to the large intestine; important for absorption of B-12

jejunum

second part of the small intestine

large intestine

digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase

enzyme that chemically breaks down lipids

liver

organ that produces bile for digestion and processes vitamins and lipids

monogastric

digestive system that consists of a single-chambered stomach

omnivore

animal that consumes both plants and animals

pancreas

gland that secretes digestive juices

pepsin

enzyme found in the stomach whose main role is protein digestion

pepsinogen

inactive form of pepsin

peristalsis

wave-like movements of muscle tissue

proventriculus

glandular part of a bird's stomach

rectum

area of the body where feces is stored until elimination

roughage

component of food that is low in energy and high in fiber

ruminant

animal with a stomach divided into four compartments

salivary amylase

enzyme found in saliva, which converts carbohydrates to maltose

small intestine

organ where digestion of protein, fats, and carbohydrates is completed

sphincter

band of muscle that controls movement of materials throughout the digestive tract

stomach

saclike organ containing acidic digestive juices

villi

folds on the inner surface of the small intestine whose role is to increase absorption area

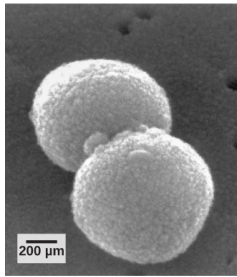
Structure of Prokaryotes

By the end of this section, you will be able to:

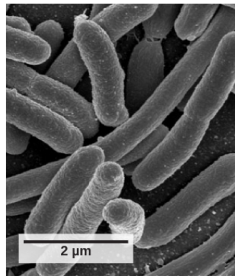
- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilli (spiral-shaped) ([\[link\]](#)).

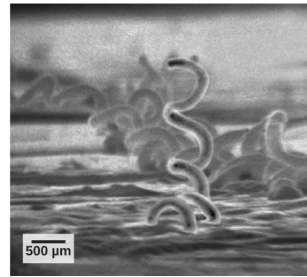
Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)



(a)



(b)



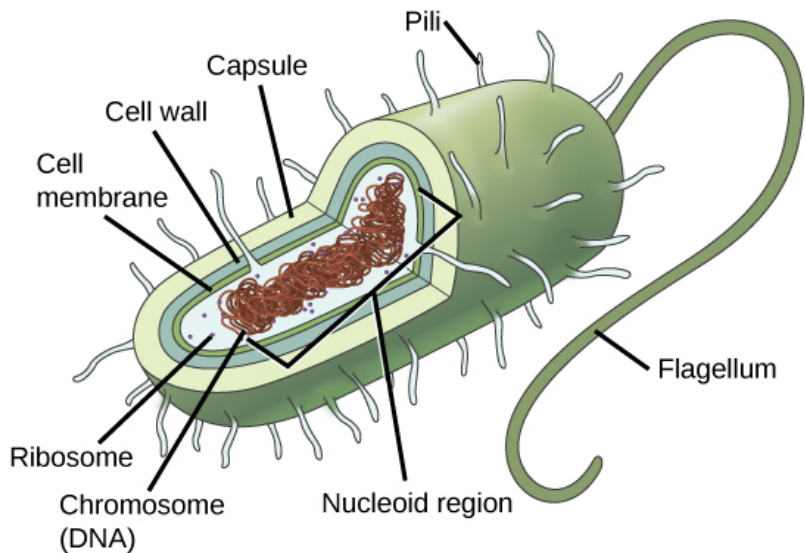
(c)

The features of a typical prokaryotic cell are shown. Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate. Phylum Proteobacteria is one of up to 52 bacteria phyla. Proteobacteria is further subdivided into five classes, Alpha through Epsilon. (credit “*Rickettsia rickettsia*”: modification of work by CDC; credit “*Spirillum minus*”: modification of work by Wolfram Adlassnig; credit “*Vibrio cholera*”: modification of work by Janice Haney Carr, CDC; credit “*Desulfovibrio vulgaris*”: modification of work by Graham Bradley; credit “*Campylobacter*”: modification of work by De Wood, Pooley, USDA, ARS, EMU; scale-bar data from Matt Russell) Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive bacteria are described in this table. Note that bacterial shape is not phylum-dependent; bacteria within a phylum may be cocci, rod-shaped, or spiral. (credit “*Chlamydia trachomatis*”: modification of work by Dr. Lance Liotta Laboratory, NCI; credit “*Treponema*

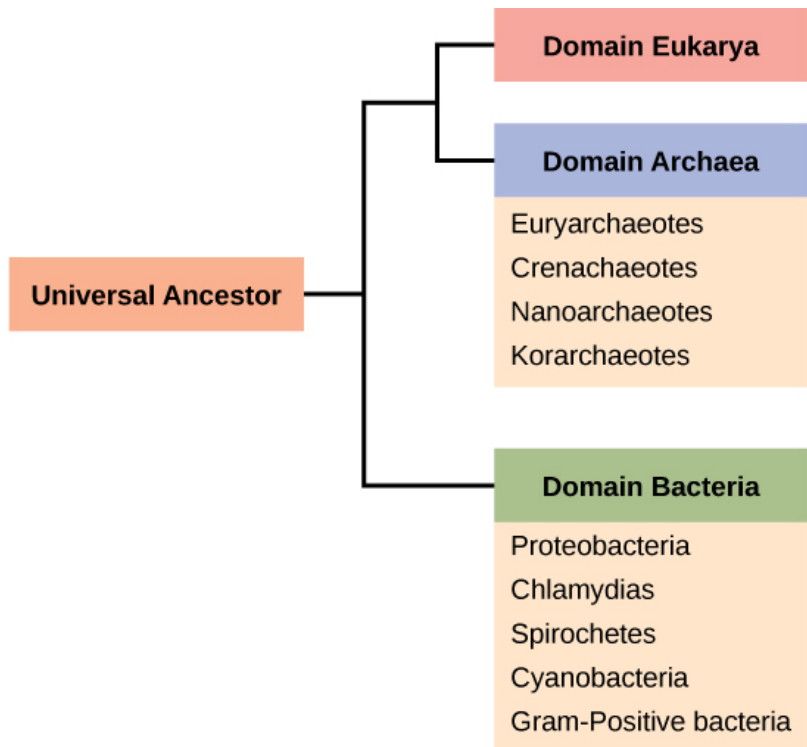
pallidum”: modification of work by Dr. David Cox, CDC; credit “Phormidium”: modification of work by USGS; credit “Clostridium difficile”: modification of work by Lois S. Wiggs, CDC; scale-bar data from Matt Russell) Archaea are separated into four phyla: the Korarchaeota, Euryarchaeota, Crenarchaeota, and Nanoarchaeota. (credit “Halobacterium”: modification of work by NASA; credit “Nanoarchaeotum equitans”: modification of work by Karl O. Stetter; credit “korarchaeota”: modification of work by Office of Science of the U.S. Dept. of Energy; scale-bar data from Matt Russell) Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Prokaryotic Cell

Recall that prokaryotes ([\[link\]](#)) are unicellular organisms that lack organelles or other internal membrane-bound structures. Therefore, they do not have a nucleus but instead generally have a single chromosome—a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.



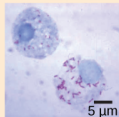
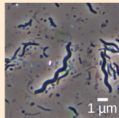
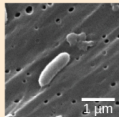
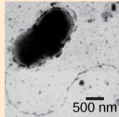

Recall that prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life ([\[link\]](#)).

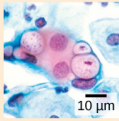
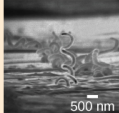
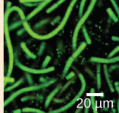
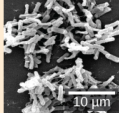



The composition of the cell wall differs significantly between the domains Bacteria and Archaea. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer, and it is responsible for the organism's shape. Some bacteria have an outer **capsule** outside the cell wall. Other structures are present in some prokaryotic species, but not in others ([\[link\]](#)). For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and makes pathogens more resistant to our immune responses. Some species

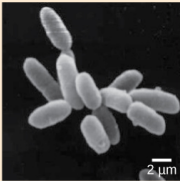
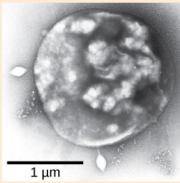
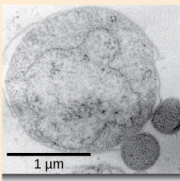
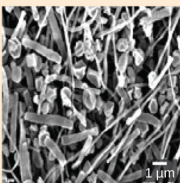
also have flagella (singular, flagellum) used for locomotion, and **pili** (singular, pilus) used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

Characteristics of phyla of Bacteria are described in [\[link\]](#) and [\[link\]](#); Archaea are described in [\[link\]](#).

Bacteria of Phylum Proteobacteria		
Class	Representative organisms	Representative micrograph
Alpha Proteobacteria Some species are photoautotrophic but some are symbionts of plants and animals and others are pathogens. Eukaryotic mitochondria are thought to be derived from bacteria in this group.	<i>Rhizobium</i> Nitrogen-fixing endosymbiont associated with the roots of legumes <i>Rickettsia</i> Obligate intracellular parasite that causes typhus and Rocky Mountain Spotted Fever (but not ricketts, which is caused by Vitamin C deficiency)	 <i>Rickettsia rickettsia</i> , stained red, grow inside a host cell.
Beta Proteobacteria This group of bacteria is diverse. Some species play an important role in the nitrogen cycle.	<i>Nitrosomas</i> Species from this group oxidize ammonia into nitrite. <i>Spirillum minus</i> Causes rat-bite fever	 <i>Spirillum minus</i>
Gamma Proteobacteria Many are beneficial symbionts that populate the human gut, but others are familiar human pathogens. Some species from this subgroup oxidize sulfur compounds.	<i>Escherichia coli</i> Normally beneficial microbe of the human gut, but some strains cause disease <i>Salmonella</i> Certain strains cause food poisoning or typhoid fever <i>Yersinia pestis</i> Causative agent of Bubonic plague <i>Pseudomonas aeruginosa</i> Causes lung infections <i>Vibrio cholera</i> Causative agent of cholera <i>Chromatium</i> Sulfur-producing bacteria that oxidize sulfur, producing H ₂ S	 <i>Vibrio cholera</i>
Delta Proteobacteria Some species generate a spore-forming fruiting body in adverse conditions. Others reduce sulfate and sulfur.	<i>Myxobacteria</i> Generate spore-forming fruiting bodies in adverse conditions <i>Desulfovibrio vulgaris</i> Anaerobic, sulfate-reducing bacterium	 <i>Desulfovibrio vulgaris</i>
Epsilon Proteobacteria Many species inhabit the digestive tract of animals as symbionts or pathogens. Bacteria from this group have been found in deep-sea hydrothermal vents and cold seep habitats.	<i>Campylobacter</i> Causes blood poisoning and intestinal inflammation <i>Helicobacter pylori</i> Causes stomach ulcers	 <i>Campylobacter</i>

Bacteria: Chlamydia, Spirochaetae, Cyanobacteria, and Gram-positive		
Phylum	Representative organisms	Representative micrograph
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cells walls lack peptidoglycan.	<i>Chlamydia trachomatis</i> Common sexually transmitted disease that can lead to blindness <i>Borrelia burgdorferi</i> Causative agent of Lyme disease	 10 µm In this pap smear, <i>Chlamydia trachomatis</i> appear as pink inclusions inside cells.
Spirochetes Most members of this species, which has spiral-shaped cells, are free-living anaerobes, but some are pathogenic. Flagella run lengthwise in the periplasmic space between the inner and outer membrane.	<i>Treponema pallidum</i> Causative agent of syphilis <i>Borrelia burgdorferi</i> Causative agent of Lyme disease	 500 nm <i>Treponema pallidum</i>
Cyanobacteria Also known as blue-green algae, these bacteria obtain their energy through photosynthesis. They are ubiquitous, found in terrestrial, marine, and freshwater environments. Eukaryotic chloroplasts are thought to be derived from bacteria in this group.	<i>Prochlorococcus</i> Believed to be the most abundant photosynthetic organism on earth; responsible for generating half the world's oxygen	 20 µm <i>Phormidium</i>
Gram-positive Bacteria Soil-dwelling members of this subgroup decompose organic matter. Some species cause disease. They have a thick cell wall and lack an outer membrane.	<i>Bacillus anthracis</i> Causes anthrax <i>Clostridium botulinum</i> Causes Botulism <i>Clostridium difficile</i> Causes diarrhea during antibiotic therapy <i>Streptomyces</i> Many antibiotics, including streptomycin, are derived from these bacteria. <i>Mycoplasmas</i> These tiny bacteria, the smallest known, lack a cell wall. Some are free-living, and some are pathogenic.	 10 µm <i>Clostridium difficile</i>

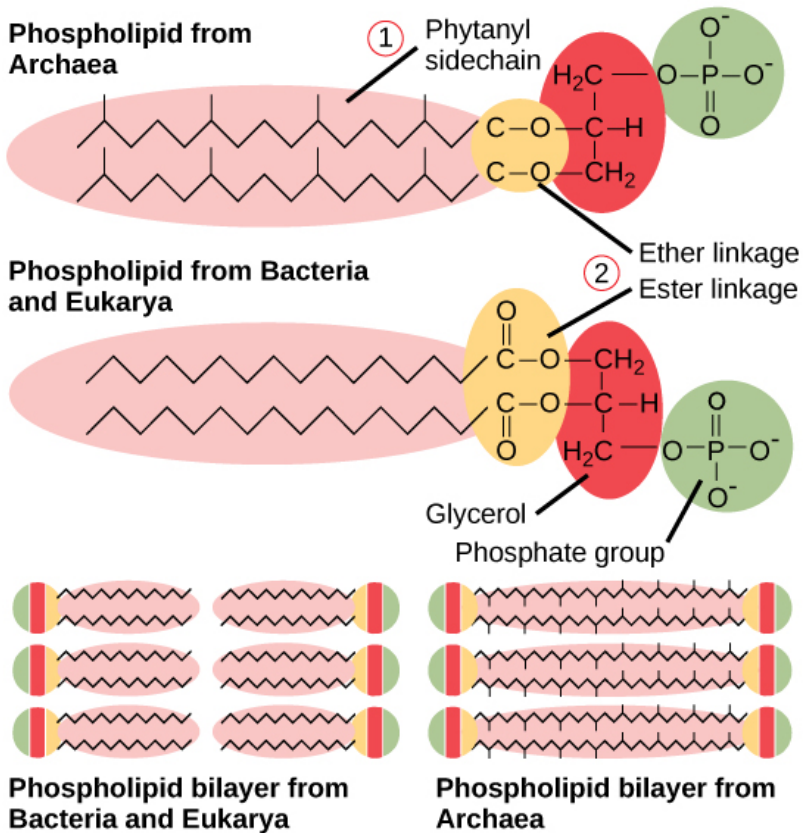
Archaea		
Phylum	Representative organisms	Representative micrograph
Euryarchaeota	Methanogens	

Archaea		
Phylum	Representative organisms	Representative micrograph
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	Methanogens Methane production causes flatulence in humans and other animals. Halobacteria Large blooms of this salt-loving archaea appear reddish due to the presence of bacteriorhodopsin in the membrane. Bacteriorhodopsin is related to the retinal pigment rhodopsin.	 <p>2 μm</p> <p><i>Halobacterium</i> strain NRC-1</p>
Crenarchaeota Members of the ubiquitous phylum play an important role in the fixation of carbon. Many members of this group are sulfur-dependent extremophiles. Some are thermophilic or hyperthermophilic.	Sulfolobus Members of this genus grow in volcanic springs at temperatures between 75° and 80°C and at a pH between 2 and 3.	 <p>1 μm</p> <p><i>Sulfolobus</i> being infected by bacteriophage</p>
Nanoarchaeota This group currently contains only one species, <i>Nanoarchaeum equitans</i> .	Nanoarchaeum equitans This species was isolated from the bottom of the Atlantic Ocean and from a hydrothermal vent at Yellowstone National Park. It is an obligate symbiont with <i>Ignicoccus</i> , another species of archaea.	 <p>1 μm</p> <p><i>Nanoarchaeum equitans</i> (small dark spheres) are in contact with their larger host, <i>Ignicoccus</i>.</p>
Korarchaeota Members of this phylum, considered to be one of the most primitive forms of life, have only been found in the Obsidian Pool, a hot spring at Yellowstone National Park.	No members of this species have been cultivated.	 <p>1 μm</p> <p>This image shows a variety of korarchaeota species from the Obsidian Pool at Yellowstone National Park.</p>

The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely surrounds the cell and separates the inside from the outside. Its selectively permeable nature keeps ions, proteins, and other molecules within the cell and prevents them from diffusing into the extracellular environment, while

other molecules may move through the membrane. Recall that the general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers ([\[link\]](#)).



The Cell Wall

The cytoplasm of prokaryotic cells has a high

concentration of dissolved solutes. Therefore, the osmotic pressure within the cell is relatively high. The cell wall is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between archaea and bacteria, and also varies between bacterial species.

Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and therefore have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. **S-layer** (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

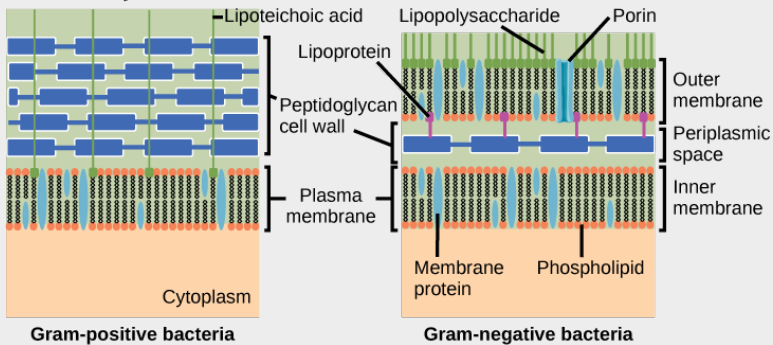
Bacteria are divided into two major groups: **Gram positive** and **Gram negative**, based on their reaction to Gram staining. Note that all Gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are Gram-negative. The Gram staining method is named after its inventor, Danish scientist Hans Christian Gram

(1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in Gram-negative organisms ([\[link\]](#)). Up to 90 percent of the cell wall in Gram-positive bacteria is composed of peptidoglycan, and most of the rest is composed of acidic substances called **teichoic acids**. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane. Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

Art Connection

Bacteria are divided into two major groups: Gram positive and Gram negative. Both groups have a cell wall composed of peptidoglycan: in Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides

and lipoproteins. Porins are proteins in this cell membrane that allow substances to pass through the outer membrane of Gram-negative bacteria. In Gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane. (credit: modification of work by "Franciscosp2"/Wikimedia Commons)



Which of the following statements is true?

1. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
2. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
3. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
4. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Archaeal cell walls do not have peptidoglycan. There are four different types of Archaeal cell walls. One type is composed of **pseudopeptidoglycan**, which is similar to peptidoglycan in morphology but contains different sugars in the polysaccharide chain. The other three types of cell walls are composed of polysaccharides, glycoproteins, or pure protein.

Structural Differences and Similarities between Bacteria and Archaea

Structural Characteristic	Bacteria	Archaea
Cell type	Prokaryotic	Prokaryotic
Cell morphology	Variable	Variable
Cell wall	Contains peptidoglycan	Does not contain peptidoglycan
Cell membrane type	Lipid bilayer	Lipid bilayer or lipid monolayer
Plasma membrane lipids	Fatty acids	Phytanyl groups

Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the sex pilus draws the two bacteria close enough to form the bridge.

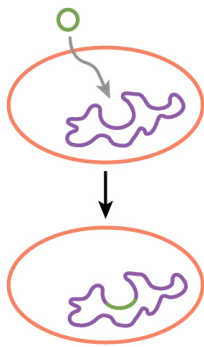
Reproduction

Reproduction in prokaryotes is asexual and usually takes place by binary fission. Recall that the DNA of a prokaryote exists as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or genetic diversity, but prokaryotes can share genes by three other mechanisms.

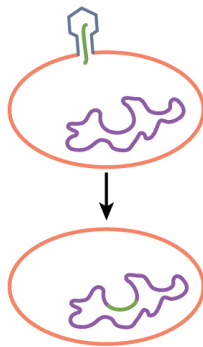
In **transformation**, the prokaryote takes in DNA

found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it too may become pathogenic. In **transduction**, bacteriophages, the viruses that infect bacteria, sometimes also move short pieces of chromosomal DNA from one bacterium to another. Transduction results in a recombinant organism. Archaea are not affected by bacteriophages but instead have their own viruses that translocate genetic material from one individual to another. In **conjugation**, DNA is transferred from one prokaryote to another by means of a pilus, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in [\[link\]](#).

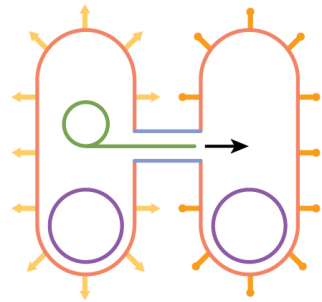
Reproduction can be very rapid: a few minutes for some species. This short generation time coupled with mechanisms of genetic recombination and high rates of mutation result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.



(a) Transformation



(b) Transduction



(c) Conjugation

Evolution Connection

The Evolution of Prokaryotes

How do scientists answer questions about the evolution of prokaryotes? Unlike with animals, artifacts in the fossil record of prokaryotes offer very little information. Fossils of ancient prokaryotes look like tiny bubbles in rock. Some scientists turn to genetics and to the principle of the molecular clock, which holds that the more recently two species have diverged, the more similar their genes (and thus proteins) will be. Conversely, species that diverged long ago will have more genes that are dissimilar.

Scientists at the NASA Astrobiology Institute and at the European Molecular Biology Laboratory collaborated to analyze the molecular evolution of 32 specific proteins common to 72 species of prokaryotes. [\[footnote\]](#) The model they derived from their data indicates that three important groups of bacteria—Actinobacteria, *Deinococcus*, and

Cyanobacteria (which the authors call *Terrabacteria*)—were the first to colonize land. (Recall that *Deinococcus* is a genus of prokaryote—a bacterium—that is highly resistant to ionizing radiation.) Cyanobacteria are photosynthesizers, while Actinobacteria are a group of very common bacteria that include species important in decomposition of organic wastes.

Battistuzzi, FU, Feijao, A, and Hedges, SB. A genomic timescale of prokaryote evolution: Insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BioMed Central: Evolutionary Biology* 4 (2004): 44, doi:10.1186/1471-2148-4-44.

The timelines of divergence suggest that bacteria (members of the domain Bacteria) diverged from common ancestral species between 2.5 and 3.2 billion years ago, whereas archaea diverged earlier: between 3.1 and 4.1 billion years ago. Eukarya later diverged off the Archaeal line. The work further suggests that stromatolites that formed prior to the advent of cyanobacteria (about 2.6 billion years ago) photosynthesized in an anoxic environment and that because of the modifications of the Terrabacteria for land (resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis using oxygen may be closely linked to adaptations to survive on land.

Section Summary

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have a cell wall that lies outside the boundary of the plasma membrane. Some prokaryotes may have additional structures such as a capsule, flagella, and pili. Bacteria and Archaea differ in the lipid composition of their cell membranes and the characteristics of the cell wall. In archaeal membranes, phytanyl units, rather than fatty acids, are linked to glycerol. Some archaeal membranes are lipid monolayers instead of bilayers.

The cell wall is located outside the cell membrane and prevents osmotic lysis. The chemical composition of cell walls varies between species. Bacterial cell walls contain peptidoglycan. Archaeal cell walls do not have peptidoglycan, but they may have pseudopeptidoglycan, polysaccharides, glycoproteins, or protein-based cell walls. Bacteria can be divided into two major groups: Gram positive and Gram negative, based on the Gram stain reaction. Gram-positive organisms have a thick cell wall, together with teichoic acids. Gram-negative organisms have a thin cell wall and an outer envelope containing lipopolysaccharides and lipoproteins.

Art Connections

[\[link\]](#) Which of the following statements is true?

1. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
2. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
3. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
4. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

[\[link\]](#) A

Review Questions

The presence of a membrane-enclosed nucleus

is a characteristic of _____.

1. prokaryotic cells
 2. eukaryotic cells
 3. all cells
 4. viruses
-

B

Which of the following consist of prokaryotic cells?

1. bacteria and fungi
 2. archaea and fungi
 3. protists and animals
 4. bacteria and archaea
-

D

The cell wall is _____.

1. interior to the cell membrane
 2. exterior to the cell membrane
 3. a part of the cell membrane
 4. interior or exterior, depending on the particular cell
-

B

Organisms most likely to be found in extreme environments are _____.

1. fungi
2. bacteria
3. viruses
4. archaea

B

Prokaryotes stain as Gram-positive or Gram-negative because of differences in the cell _____.

1. wall
2. cytoplasm
3. nucleus
4. chromosome

A

Pseudopeptidoglycan is a characteristic of the walls of _____.

1. eukaryotic cells
2. bacterial prokaryotic cells

3. archaean prokaryotic cells
 4. bacterial and archaean prokaryotic cells
-

C

The lipopolysaccharide layer (LPS) is a characteristic of the wall of _____.

1. archaean cells
 2. Gram-negative bacteria
 3. bacterial prokaryotic cells
 4. eukaryotic cells
-

B

Free Response

Mention three differences between bacteria and archaea.

Responses will vary. A possible answer is: Bacteria contain peptidoglycan in the cell wall; archaea do not. The cell membrane in bacteria is a lipid bilayer; in archaea, it can be a lipid bilayer or a monolayer. Bacteria contain fatty

acids on the cell membrane, whereas archaea contain phytanyl.

Explain the statement that both types, bacteria and archaea, have the same basic structures, but built from different chemical components.

Both bacteria and archaea have cell membranes and they both contain a hydrophobic portion. In the case of bacteria, it is a fatty acid; in the case of archaea, it is a hydrocarbon (phytanyl). Both bacteria and archaea have a cell wall that protects them. In the case of bacteria, it is composed of peptidoglycan, whereas in the case of archaea, it is pseudopeptidoglycan, polysaccharides, glycoproteins, or pure protein. Bacterial and archaeal flagella also differ in their chemical structure.

Glossary

capsule

external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

conjugation

process by which prokaryotes move DNA from one individual to another using a pilus

Gram negative

bacterium whose cell wall contains little peptidoglycan but has an outer membrane

Gram positive

bacterium that contains mainly peptidoglycan in its cell walls

peptidoglycan

material composed of polysaccharide chains cross-linked to unusual peptides

pilus

surface appendage of some prokaryotes used for attachment to surfaces including other prokaryotes

pseudopeptidoglycan

component of archaea cell walls that is similar to peptidoglycan in morphology but contains different sugars

S-layer

surface-layer protein present on the outside of cell walls of archaea and bacteria

teichoic acid

polymer associated with the cell wall of Gram-positive bacteria

transduction

process by which a bacteriophage moves DNA

from one prokaryote to another

transformation

process by which a prokaryote takes in DNA found in its environment that is shed by other prokaryotes

Viral Evolution, Morphology, and Classification

By the end of this section, you will be able to:

- Describe how viruses were first discovered and how they are detected
- Discuss three hypotheses about how viruses evolved
- Recognize the basic shapes of viruses
- Understand past and emerging classification systems for viruses

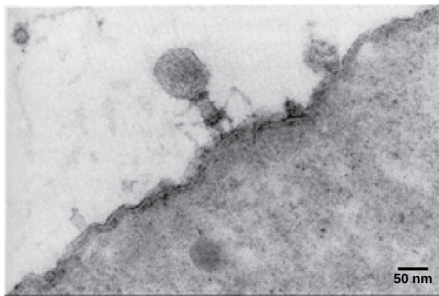
Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown. In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these *E. coli* cells are dwarfed by cultured colon cells. (credit a: modification of work by U.S. Dept. of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. Nataro and S. Sears, unpub. data, CDC; scale-bar data from Matt Russell)

Discovery and Detection

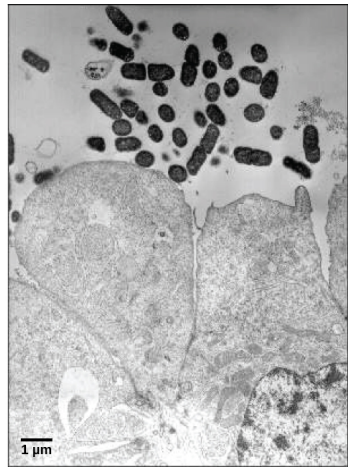
Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these “filterable” infectious agents were not simply very small bacteria but were a new type of very small, disease-causing particle.

Virions, single virus particles, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100-times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family. It was not until the development of the electron microscope in the late 1930s that scientists got their first good view of the structure of the tobacco mosaic virus (TMV) ([\[link\]](#)) and other viruses ([\[link\]](#)). The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope.

The use of these technologies has allowed for the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.



(a)



(b)

Evolution of Viruses

Although biologists have accumulated a significant amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar historic evidence. However, viruses do not fossilize,

so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses don't have a single common ancestor, scholars have yet to find a single hypothesis about virus origins that is fully accepted in the field. One such hypothesis, called devolution or the regressive hypothesis, proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery. A second hypothesis (called escapist or the progressive hypothesis) accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, likely evolving alongside the cells they rely on as hosts; studies of some plant pathogens support this hypothesis.

As technology advances, scientists may develop and refine further hypotheses to explain the origin of viruses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to

advances in the treatments for the ailments they produce.

The KSHV virus binds the xCT receptor on the surface of human cells. xCT receptors protect cells against stress. Stressed cells express more xCT receptors than non-stressed cells. The KSHV virion causes cells to become stressed, thereby increasing expression of the receptor to which it binds. (credit: modification of work by NIAID, NIH)

Viral Morphology

Viruses are **acellular**, meaning they are biological entities that do not have a cellular structure. They therefore lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes an outer **envelope** made of protein and phospholipid membranes derived from the host cell. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate with the complexity of the virion. Some of the most complex virion structures are observed in bacteriophages, viruses that infect the simplest living organisms, bacteria.

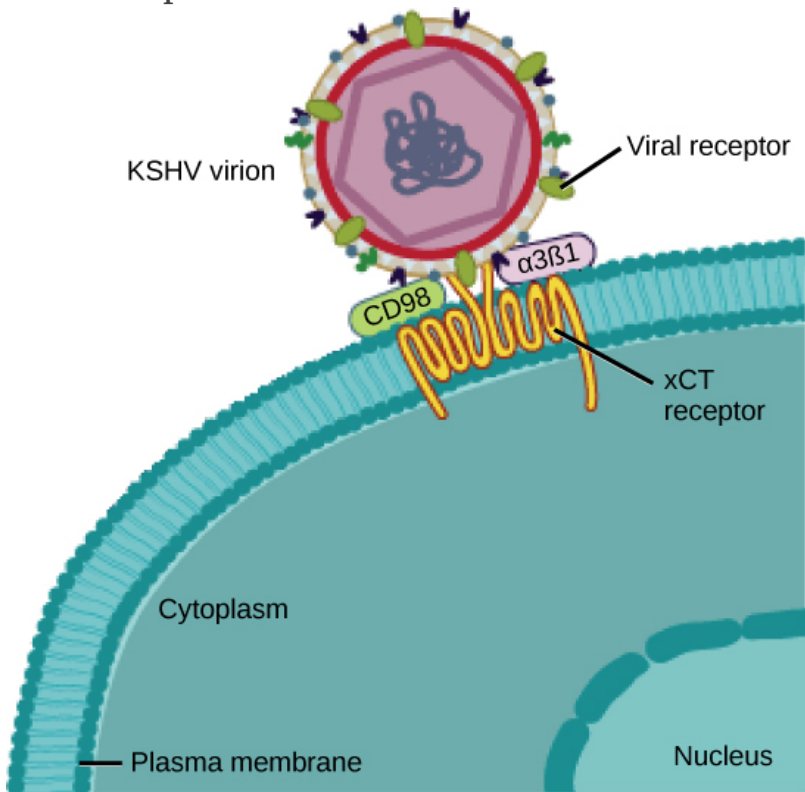
Morphology

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. All virions have a nucleic acid genome covered by a protective layer of proteins, called a **capsid**. The capsid is made up of protein subunits called **capsomeres**. Some viral capsids are simple polyhedral “spheres,” whereas others are quite complex in structure.

In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

Many viruses use some sort of glycoprotein to attach to their host cells via molecules on the cell called **viral receptors** ([\[link\]](#)). For these viruses, attachment is a requirement for later penetration of the cell membrane, so they can complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell

surfaces and have their own physiological functions. Viruses have simply evolved to make use of these molecules for their own replication. For example, HIV uses the CD4 molecule on T lymphocytes as one of its receptors. CD4 is a type of molecule called a cell adhesion molecule, which functions to keep different types of immune cells in close proximity to each other during the generation of a T lymphocyte immune response.



Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses

its DNA.

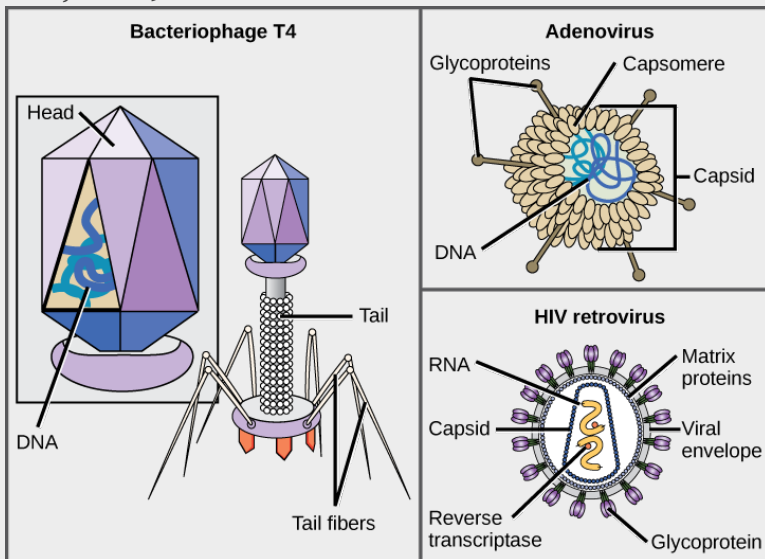
Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans, uses glycoprotein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

Enveloped virions like HIV, the causative agent in AIDS, consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins. Glycoproteins embedded in the viral envelope are used to attach to host cells. Other envelope proteins are the **matrix proteins** that stabilize the envelope and often play a role in the assembly of progeny virions. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification ([\[link\]](#)).

Art Connection

Viruses can be either complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. (credit “bacteriophage, adenovirus”: modification of work by NCBI, NIH; credit “HIV retrovirus”: modification of work by NIAID, NIH)



Which of the following statements about virus structure is true?

1. All viruses are encased in a viral membrane.
2. The capsomere is made up of small protein

subunits called capsids.

3. DNA is the genetic material in all viruses.

4. Glycoproteins help the virus attach to the host cell.

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. The **virus core** contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot get from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell,

the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases, and therefore often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid. Rabies transmission occurs when saliva from an infected mammal enters a wound. The virus travels through neurons in the peripheral nervous system to the central nervous system where it impairs brain function, and then travels to other tissues. The virus can infect any mammal, and most die within weeks of infection. Smallpox is a human virus transmitted by inhalation of the variola virus, localized in the skin, mouth, and throat, which causes a characteristic rash. Before its eradication in 1979, infection resulted in a 30–35 percent mortality rate. (credit “rabies diagram”: modification of work by CDC; “rabies micrograph”: modification of work by Dr. Fred Murphy, CDC; credit “small pox

micrograph”: modification of work by Dr. Fred Murphy, Sylvia Whitfield, CDC; credit “smallpox photo”: modification of work by CDC; scale-bar data from Matt Russell) Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections. (credit “adenovirus”: modification of work by Dr. Richard Feldmann, National Cancer Institute; credit “micrograph”: modification of work by Dr. G. William Gary, Jr., CDC; scale-bar data from Matt Russell) Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex. (credit a: modification of work by Dr. Fred Murphy, Sylvia Whitfield; credit b: modification of work by Liza Gross; credit c: modification of work by Dr. F. A. Murphy, CDC; credit d: modification of work by USDA ARS; credit e: modification of work by Linda Stannard, Department of Medical Microbiology, University of Cape Town, South Africa, NASA; scale-bar data from Matt Russell)

Virus Classification

To understand the features shared among different groups of viruses, a classification scheme is necessary. As most viruses are not thought to have evolved from a common ancestor, however, the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the different viruses. However, these earlier classification methods grouped viruses differently, based on which features of the virus they were using to classify them. The most commonly used classification method today is called the Baltimore classification scheme and is based on how messenger RNA (mRNA) is generated in each particular type of virus.

Past Systems of Classification

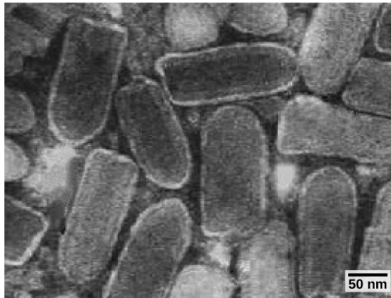
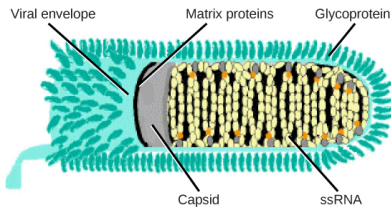
Viruses are classified in several ways: by factors such as their core content ([\[link\]](#) and [\[link\]](#)), the structure of their capsids, and whether they have an outer envelope. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Virus Classification by Genome Structure and Core

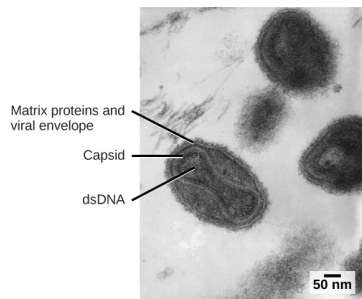
Core Classifications

Examples

- **RNA**: Rabies virus, retroviruses
- **Double stranded**: Herpesviruses, smallpox virus
- **Single stranded**: Retroviruses
- **Double stranded**: Herpesviruses, smallpox virus
- **Rabies virus, retroviruses, herpesviruses, smallpox virus**
- **Papillomaviruses, many bacteriophages**
- **Non-segmented genome consists of a single segment of genetic material**
- **Segmented: genome is divided into multiple segments**



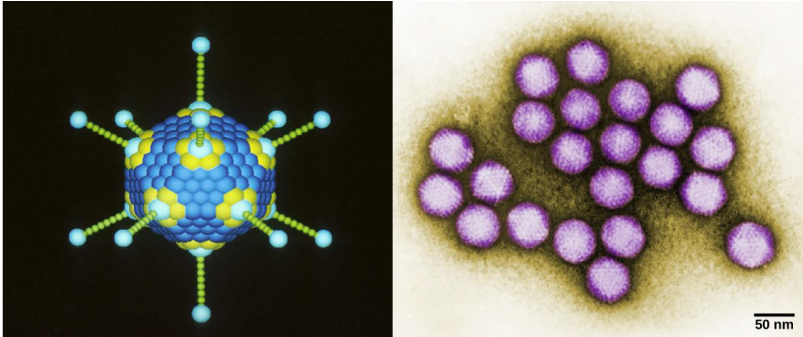
(a) Rabies virus



(b) Variola virus

Viruses can also be classified by the design of their capsids ([\[link\]](#) and [\[link\]](#)). Capsids are classified as

naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex ([link] and [link]). The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures ([link]).



**Virus Classification by
Capsid Structure**

Capsid Classification
Naked icosahedral

Enveloped icosahedral

Enveloped helical

Examples

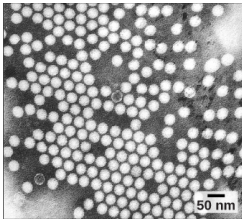
Hepatitis A virus,
polioviruses

Epstein-Barr virus, herpes
simplex virus, rubella
virus, yellow fever virus,
HIV 1

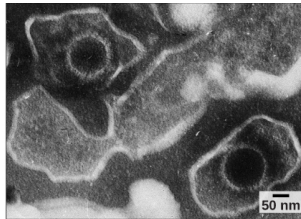
Influenza viruses, mumps
virus, measles virus,

Naked helical
Complex with many
proteins; some have
combinations of
icosahedral and helical
capsid structures

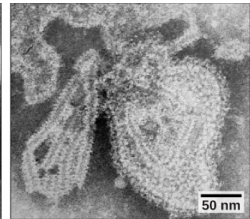
rabies virus
Tobacco mosaic virus
Herpesviruses, smallpox
virus, hepatitis B virus, T4
bacteriophage



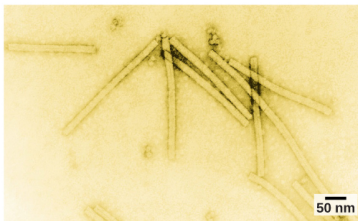
(a)



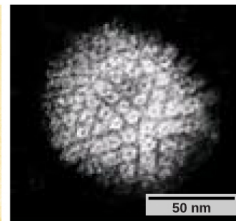
(b)



(c)



(d)



(e)

Baltimore Classification

The most commonly used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In addition to the differences in morphology and genetics mentioned above, the Baltimore classification scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus.

Group I viruses contain double-stranded DNA (dsDNA) as their genome. Their mRNA is produced by transcription in much the same way as with cellular DNA. **Group II** viruses have single-stranded DNA (ssDNA) as their genome. They convert their single-stranded genomes into a dsDNA intermediate before transcription to mRNA can occur. **Group III** viruses use dsRNA as their genome. The strands separate, and one of them is used as a template for the generation of mRNA using the RNA-dependent RNA polymerase encoded by the virus. **Group IV** viruses have ssRNA as their genome with a positive polarity. **Positive polarity** means that the genomic RNA can serve directly as mRNA. Intermediates of dsRNA, called **replicative intermediates**, are made in the process of copying the genomic RNA. Multiple, full-length RNA strands of negative polarity (complimentary to the positive-stranded genomic RNA) are formed from these intermediates, which may then serve as templates for the production of RNA with positive polarity, including both full-length genomic RNA and shorter viral mRNAs. **Group V** viruses contain ssRNA genomes with a **negative polarity**, meaning that their sequence is complementary to the mRNA. As with Group IV viruses, dsRNA intermediates are used to make copies of the genome and produce mRNA. In this case, the negative-stranded genome can be converted directly to mRNA. Additionally, full-length positive RNA strands are made to serve as templates for the production of the negative-

stranded genome. **Group VI** viruses have diploid (two copies) ssRNA genomes that must be converted, using the enzyme **reverse transcriptase**, to dsDNA; the dsDNA is then transported to the nucleus of the host cell and inserted into the host genome. Then, mRNA can be produced by transcription of the viral DNA that was integrated into the host genome. **Group VII** viruses have partial dsDNA genomes and make ssRNA intermediates that act as mRNA, but are also converted back into dsDNA genomes by reverse transcriptase, necessary for genome replication. The characteristics of each group in the Baltimore classification are summarized in [\[link\]](#) with examples of each group.

Baltimore Classification			
Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-	DNA is	Canine

	stranded DNA	converted to double-stranded form before RNA is transcribed	parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (picornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated	Human immunodeficiency virus (HIV)

VII	Double stranded DNA viruses with reverse transcriptase	DNA The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)
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Section Summary

Viruses are tiny, acellular entities that can usually only be seen with an electron microscope. Their genomes contain either DNA or RNA—never both—and they replicate using the replication proteins of a host cell. Viruses are diverse, infecting archaea, bacteria, fungi, plants, and animals. Viruses consist of a nucleic acid core surrounded by a protein capsid with or without an outer lipid envelope. The capsid shape, presence of an envelope, and core

composition dictate some elements of the classification of viruses. The most commonly used classification method, the Baltimore classification, categorizes viruses based on how they produce their mRNA.

Art Connections

[\[link\]](#) Which of the following statements about virus structure is true?

1. All viruses are encased in a viral membrane.
2. The capsomere is made up of small protein subunits called capsids.
3. DNA is the genetic material in all viruses.
4. Glycoproteins help the virus attach to the host cell.

[\[link\]](#) D

Review Questions

Which statement is true?

1. A virion contains DNA and RNA.
 2. Viruses are acellular.
 3. Viruses replicate outside of the cell.
 4. Most viruses are easily visualized with a light microscope.
-

B

The viral _____ plays a role in attaching a virion to the host cell.

1. core
 2. capsid
 3. envelope
 4. both b and c
-

D

Viruses_____.

1. all have a round shape
 2. cannot have a long shape
 3. do not maintain any shape
 4. vary in shape
-

D

Free Response

The first electron micrograph of a virus (tobacco mosaic virus) was produced in 1939. Before that time, how did scientists know that viruses existed if they could not see them? (Hint: Early scientists called viruses “filterable agents.”)

Viruses pass through filters that eliminated all bacteria that were visible in the light microscopes at the time. As the bacteria-free filtrate could still cause infections when given to a healthy organism, this observation demonstrated the existence of very small infectious agents. These agents were later shown to be unrelated to bacteria and were classified as viruses.

Glossary

acellular

lacking cells

capsid

protein coating of the viral core

capsomere

protein subunit that makes up the capsid

envelope

lipid bilayer that envelopes some viruses

group I virus

virus with a dsDNA genome

group II virus

virus with a ssDNA genome

group III virus

virus with a dsRNA genome

group IV virus

virus with a ssRNA genome with positive polarity

group V virus

virus with a ssRNA genome with negative polarity

group VI virus

virus with a ssRNA genomes converted into dsDNA by reverse transcriptase

group VII virus

virus with a single-stranded mRNA converted into dsDNA for genome replication

matrix protein

envelope protein that stabilizes the envelope and often plays a role in the assembly of

progeny virions

negative polarity

ssRNA viruses with genomes complimentary to their mRNA

positive polarity

ssRNA virus with a genome that contains the same base sequences and codons found in their mRNA

replicative intermediate

dsRNA intermediate made in the process of copying genomic RNA

reverse transcriptase

enzyme found in Baltimore groups VI and VII that converts single-stranded RNA into double-stranded DNA

viral receptor

glycoprotein used to attach a virus to host cells via molecules on the cell

virion

individual virus particle outside a host cell

virus core

contains the virus genome

Virus Infections and Hosts

By the end of this section, you will be able to:

- List the steps of replication and explain what occurs at each step
- Describe the lytic and lysogenic cycles of virus replication
- Explain the transmission and diseases of animal and plant viruses
- Discuss the economic impact of animal and plant viruses

Viruses can be seen as obligate, intracellular parasites. A virus must attach to a living cell, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so that the virus can infect other cells. Viruses can infect only certain species of hosts and only certain cells within that host. Cells that a virus may use to replicate are called **permissive**. For most viruses, the molecular basis for this specificity is that a particular surface molecule known as the viral receptor must be found on the host cell surface for the virus to attach. Also, metabolic and host cell immune response differences seen in different cell types based on differential gene expression are a likely factor in which cells a virus may target for replication. The permissive cell must make the substances that the virus needs or the virus will not be able to replicate there.

Steps of Virus Infections

A virus must use cell processes to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called **cytopathic** (causing cell damage) effects, can change cell functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through **lysis** (bursting) or apoptosis (programmed cell death or “cell suicide”), releasing all progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as **budding**, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that the virus infects may make it impossible for the cells to function normally, even though the cells remain alive for a period of time. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release ([link]).

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host—and the cells within the host—that can be infected by a particular virus. This can be illustrated by thinking of several keys and several locks, where each key will fit only one specific lock.

Link to Learning



This [video](#) explains how influenza attacks the body.

Entry

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the

cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded, and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is transcribed to messenger RNA (mRNA), which is then used to direct protein synthesis. RNA viruses usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA directs the host cell to synthesize viral enzymes and capsid proteins, and assemble new virions. Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins.

Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed into DNA, which then is incorporated into the host cell genome. They are within group VI of the Baltimore classification scheme. To convert RNA into DNA, retroviruses must contain genes that encode the virus-specific enzyme reverse transcriptase that transcribes an RNA template to DNA. Reverse transcription never occurs in uninfected host cells—the needed enzyme reverse transcriptase is only derived from the

expression of viral genes within the infected host cells. The fact that HIV produces some of its own enzymes not found in the host has allowed researchers to develop drugs that inhibit these enzymes. These drugs, including the reverse transcriptase inhibitor **AZT**, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

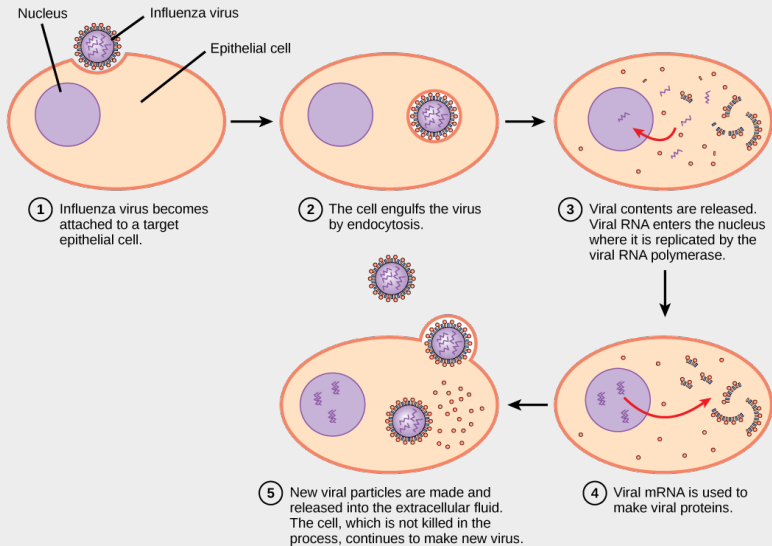
Egress

The last stage of viral replication is the release of the new virions produced in the host organism, where they are able to infect adjacent cells and repeat the replication cycle. As you've learned, some viruses are released when the host cell dies, and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Art Connection

In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and

assembled into new virions.



Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Link to Learning



Watch a [video](#) on viruses, identifying structures,

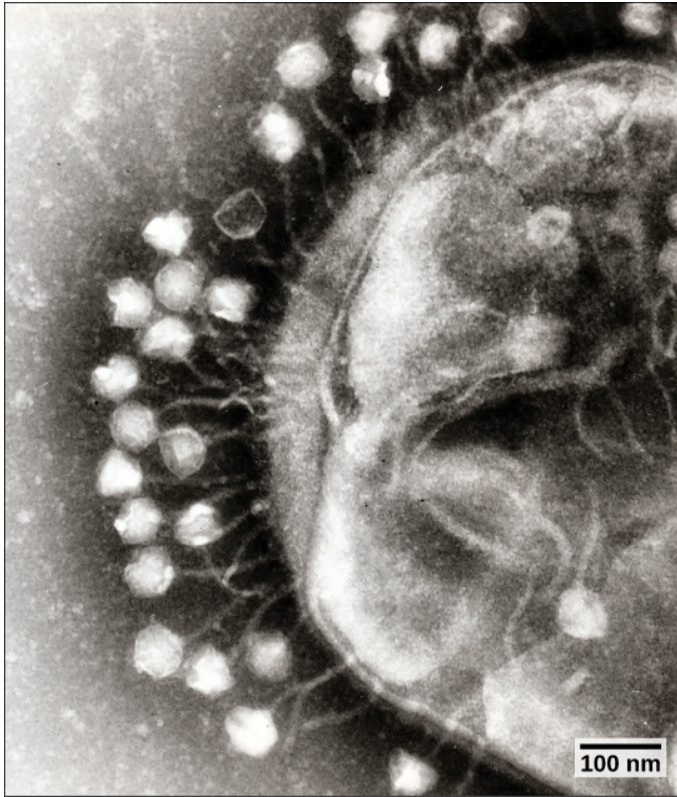
modes of transmission, replication, and more.

Different Hosts and Their Viruses

As you've learned, viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on Earth. On the other hand, so many different types of viruses exist on Earth that nearly every living organism has its own set of viruses that tries to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses.

This transmission electron micrograph shows bacteriophages attached to a bacterial cell. (credit: modification of work by Dr. Graham Beards; scale-bar data from Matt Russell)

Bacteriophages

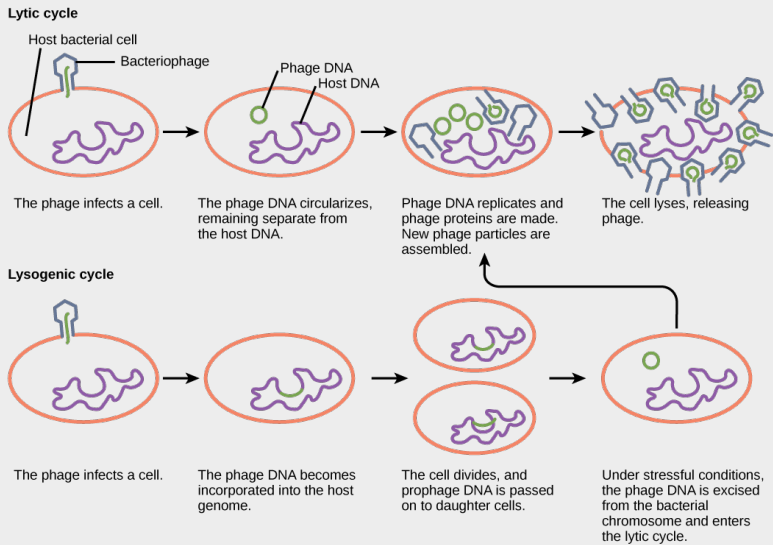


Bacteriophages are viruses that infect bacteria ([link]). When infection of a cell by a bacteriophage results in the production of new virions, the infection is said to be **productive**. If the virions are released by bursting the cell, the virus replicates by means of a **lytic cycle** ([link]). An example of a lytic bacteriophage is T4, which infects *Escherichia coli* found in the human intestinal tract. Sometimes, however, a virus can remain within the cell without being released. For example, when a temperate bacteriophage infects a bacterial cell, it replicates by means of a **lysogenic cycle** ([link]), and the viral genome is incorporated into the genome of the host

cell. When the phage DNA is incorporated into the host cell genome, it is called a **prophage**. An example of a lysogenic bacteriophage is the λ (lambda) virus, which also infects the *E. coli* bacterium. Viruses that infect plant or animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpesviruses, including herpes simplex viruses, the cause of oral and genital herpes in humans. In a process called **latency**, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages. Latency will be described in more detail below.

Art Connection

A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.



Which of the following statements is false?

1. In the lytic cycle, new phage are produced and released into the environment.
2. In the lysogenic cycle, phage DNA is incorporated into the host genome.
3. An environmental stressor can cause the phage to initiate the lysogenic cycle.
4. Cell lysis only occurs in the lytic cycle.

(a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome becomes incorporated in the host DNA and can reactivate after latency in the form of (b) shingles, often exhibiting a rash.
(credit a: modification of work by Dr. Erskine

Palmer, B. G. Martin, CDC; credit b: modification of work by “rosmary”/Flickr; scale-bar data from Matt Russell) HPV, or human papillomavirus, has a naked icosahedral capsid visible in this transmission electron micrograph and a double-stranded DNA genome that is incorporated into the host DNA. The virus, which is sexually transmitted, is oncogenic and can lead to cervical cancer. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Animal Viruses

Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or “naked” animal viruses may enter cells in two different ways. As a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then “injected” into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis, or **fusion**. Many enveloped viruses enter the cell by

receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. As we have already discussed using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell's plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

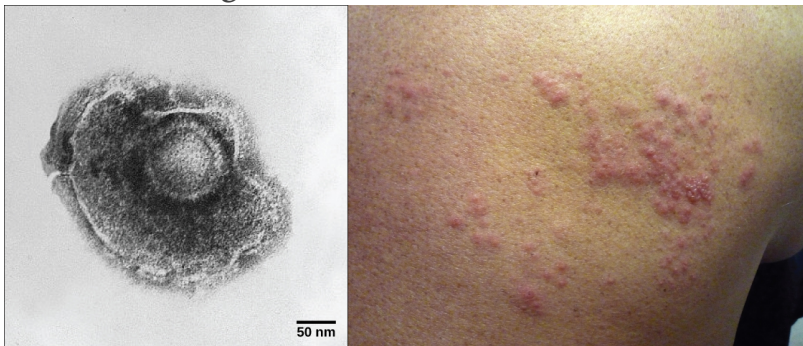
As you will learn in the next module, animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of **acute disease**, where symptoms get increasingly worse for a short period followed by the elimination of the virus from the body by the immune system and eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term **chronic infections**, such as the virus causing hepatitis C,

whereas others, like herpes simplex virus, only cause **intermittent** symptoms. Still other viruses, such as human herpesviruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host, and thus we say these patients have an **asymptomatic infection**.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, and many infections are detected only by routine blood work on patients with risk factors such as intravenous drug use. On the other hand, since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows for the virus to escape elimination by the immune system and persist in individuals for years, all the while producing low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As already discussed, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus “hides” in the

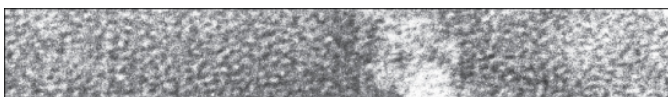
tissue and makes few if any viral proteins, there is nothing for the immune response to act against, and immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpesviruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as “shingles” ([link](#)ab).

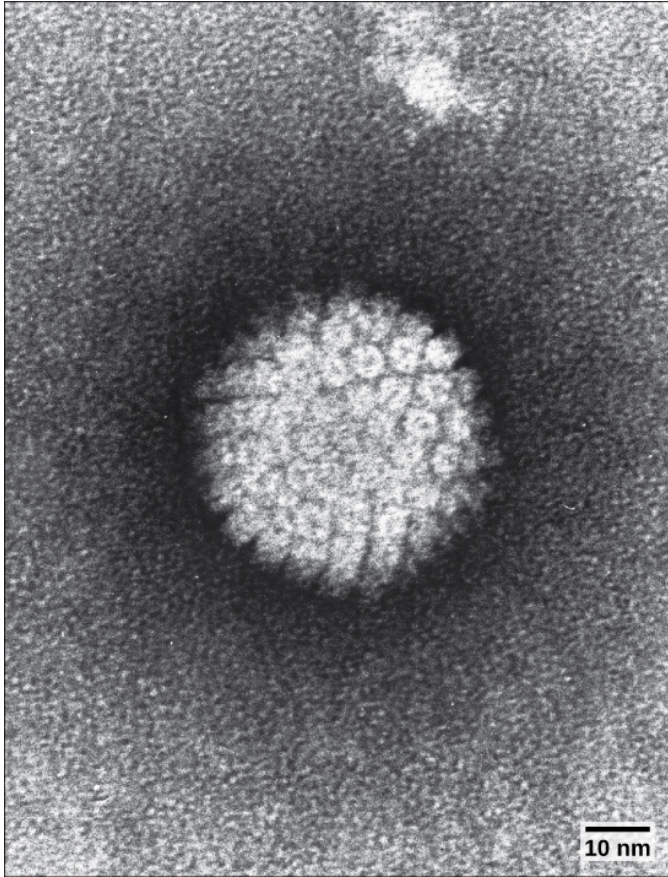


(a)

(b)

Some animal-infecting viruses, including the hepatitis C virus discussed above, are known as **oncogenic viruses**: They have the ability to cause cancer. These viruses interfere with the normal regulation of the host cell cycle either by either introducing genes that stimulate unregulated cell growth (oncogenes) or by interfering with the expression of genes that inhibit cell growth. Oncogenic viruses can be either DNA or RNA viruses. Cancers known to be associated with viral infections include cervical cancer caused by human papillomavirus (HPV) ([\[link\]](#)), liver cancer caused by hepatitis B virus, T-cell leukemia, and several types of lymphoma.





Link to Learning



Visit the interactive [animations](#) showing the various stages of the replicative cycles of animal viruses and click on the flash animation links.

Plant Viruses

Plant viruses, like other viruses, contain a core of either DNA or RNA. You have already learned about one of these, the tobacco mosaic virus. As plant cells have a cell wall to protect their cells, these viruses do not use receptor-mediated endocytosis to enter host cells as is seen with animal viruses. For many plant viruses to be transferred from plant to plant, damage to some of the plants' cells must occur to allow the virus to enter a new host. This damage is often caused by weather, insects, animals, fire, or human activities like farming or landscaping. Additionally, plant offspring may inherit viral diseases from parent plants. Plant viruses can be transmitted by a variety of vectors, through contact with an infected plant's sap, by living organisms such as insects and nematodes, and through pollen. When plants viruses are transferred between different plants, this is known as **horizontal transmission**, and when they are inherited from a parent, this is called **vertical transmission**.

Symptoms of viral diseases vary according to the virus and its host ([\[link\]](#)). One common symptom is **hyperplasia**, the abnormal proliferation of cells that causes the appearance of plant tumors known as **galls**. Other viruses induce **hypoplasia**, or decreased cell growth, in the leaves of plants, causing thin, yellow areas to appear. Still other viruses affect the plant by directly killing plant cells, a process known as **cell necrosis**. Other symptoms of plant viruses include malformed leaves, black streaks on the stems of the plants, altered growth of stems, leaves, or fruits, and ring spots, which are circular or linear areas of discoloration found in a leaf.

**Some Common
Symptoms of Plant Viral
Diseases**

Symptom

Hyperplasia

Hypoplasia

Cell necrosis

Abnormal growth
patterns

Discoloration

Appears as

Galls (tumors)

Thinned, yellow splotches
on leaves

Dead, blackened stems,
leaves, or fruit

Malformed stems, leaves,
or fruit

Yellow, red, or black

	lines, or rings in stems, leaves, or fruit	
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Plant viruses can seriously disrupt crop growth and development, significantly affecting our food supply. They are responsible for poor crop quality and quantity globally, and can bring about huge economic losses annually. Others viruses may damage plants used in landscaping. Some viruses that infect agricultural food plants include the name of the plant they infect, such as tomato spotted wilt virus, bean common mosaic virus, and cucumber mosaic virus. In plants used for landscaping, two of the most common viruses are peony ring spot and rose mosaic virus. There are far too many plant viruses to discuss each in detail, but symptoms of bean common mosaic virus result in lowered bean production and stunted, unproductive plants. In the ornamental rose, the rose mosaic disease causes wavy yellow lines and colored splotches on the leaves of the plant.

Section Summary

Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. A

viral infection may be productive, resulting in new virions, or nonproductive, which means that the virus remains inside the cell without producing new virions. Bacteriophages are viruses that infect bacteria. They have two different modes of replication: the lytic cycle, where the virus replicates and bursts out of the bacteria, and the lysogenic cycle, which involves the incorporation of the viral genome into the bacterial host genome. Animal viruses cause a variety of infections, with some causing chronic symptoms (hepatitis C), some intermittent symptoms (latent viruses such as herpes simplex virus 1), and others that cause very few symptoms, if any (human herpesviruses 6 and 7). Oncogenic viruses in animals have the ability to cause cancer by interfering with the regulation of the host cell cycle. Viruses of plants are responsible for significant economic damage in both agriculture and plants used for ornamentation.

Art Connections

[\[link\]](#) Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

[\[link\]](#) The host cell can continue to make new virus particles.

[\[link\]](#) Which of the following statements is false?

1. In the lytic cycle, new phage are produced and released into the environment.
2. In the lysogenic cycle, phage DNA is incorporated into the host genome.
3. An environmental stressor can cause the phage to initiate the lysogenic cycle.
4. Cell lysis only occurs in the lytic cycle.

[\[link\]](#) C

Review Questions

Which statement is *not* true of viral replication?

1. A lysogenic cycle kills the host cell.
2. There are six basic steps in the viral replication cycle.
3. Viral replication does not affect host cell function.
4. Newly released virions can infect adjacent

cells.

D

Which statement is true of viral replication?

1. In the process of apoptosis, the cell survives.
 2. During attachment, the virus attaches at specific sites on the cell surface.
 3. The viral capsid helps the host cell produce more copies of the viral genome.
 4. mRNA works outside of the host cell to produce enzymes and proteins.
-

B

Which statement is true of reverse transcriptase?

1. It is a nucleic acid.
 2. It infects cells.
 3. It transcribes RNA to make DNA.
 4. It is a lipid.
-

C

Oncogenic virus cores can be_____.

1. RNA
 2. DNA
 3. neither RNA nor DNA
 4. either RNA or DNA
-

D

Which is true of DNA viruses?

1. They use the host cell's machinery to produce new copies of their genome.
 2. They all have envelopes.
 3. They are the only kind of viruses that can cause cancer.
 4. They are not important plant pathogens.
-

A

A bacteriophage can infect _____.

1. the lungs
 2. viruses
 3. prions
 4. bacteria
-

Free Response

Why can't dogs catch the measles?

The virus can't attach to dog cells, because dog cells do not express the receptors for the virus and/or there is no cell within the dog that is permissive for viral replication.

One of the first and most important targets for drugs to fight infection with HIV (a retrovirus) is the reverse transcriptase enzyme. Why?

Reverse transcriptase is needed to make more HIV-1 viruses, so targeting the reverse transcriptase enzyme may be a way to inhibit the replication of the virus. Importantly, by targeting reverse transcriptase, we do little harm to the host cell, since host cells do not make reverse transcriptase. Thus, we can specifically attack the virus and not the host cell when we use reverse transcriptase inhibitors.

In this section, you were introduced to different types of viruses and viral diseases. Briefly discuss the most interesting or surprising thing you learned about viruses.

Answer is open and will vary.

Although plant viruses cannot infect humans, what are some of the ways in which they affect humans?

Plant viruses infect crops, causing crop damage and failure, and considerable economic losses.

Glossary

acute disease

disease where the symptoms rise and fall within a short period of time

asymptomatic disease

disease where there are no symptoms and the individual is unaware of being infected unless lab tests are performed

AZT

anti-HIV drug that inhibits the viral enzyme reverse transcriptase

bacteriophage

virus that infects bacteria

budding

method of exit from the cell used in certain animal viruses, where virions leave the cell individually by capturing a piece of the host plasma membrane

cell necrosis

cell death

chronic infection

describes when the virus persists in the body for a long period of time

cytopathic

causing cell damage

fusion

method of entry by some enveloped viruses, where the viral envelope fuses with the plasma membrane of the host cell

gall

appearance of a plant tumor

horizontal transmission

transmission of a disease between unrelated individuals

hyperplasia

abnormally high cell growth and division

hypoplasia

abnormally low cell growth and division

intermittent symptom

symptom that occurs periodically

latency

virus that remains in the body for a long period of time but only causes intermittent symptoms

lysis

bursting of a cell

lytic cycle

type of virus replication in which virions are released through lysis, or bursting, of the cell

lysogenic cycle

type of virus replication in which the viral genome is incorporated into the genome of the host cell

oncogenic virus

virus that has the ability to cause cancer

permissive

cell type that is able to support productive replication of a virus

productive

viral infection that leads to the production of new virions

prophage

phage DNA that is incorporated into the host cell genome

vertical transmission

transmission of disease from parent to offspring

The Scope of Ecology

By the end of this section, you will be able to:

- Define ecology and the four levels of ecological research
- Describe examples of the ways in which ecology requires the integration of different scientific disciplines
- Distinguish between abiotic and biotic components of the environment
- Recognize the relationship between abiotic and biotic components of the environment

Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models.

Link to Learning



Climate change can alter where organisms live, which can sometimes directly affect human health. Watch the PBS video “[Feeling the Effects of Climate Change](#)” in which researchers discover a pathogenic organism living far outside of its normal range.

Ecologists study within several biological levels of organization. (credit “organisms”: modification of work by "Crystl"/Flickr; credit “ecosystems”: modification of work by Tom Carlisle, US Fish and Wildlife Service Headquarters; credit “biosphere”: NASA)

Levels of Ecological Study

When a discipline such as biology is studied, it is often helpful to subdivide it into smaller, related areas. For instance, cell biologists interested in cell signaling need to understand the chemistry of the signal molecules (which are usually proteins) as well as the result of cell signaling. Ecologists interested in the factors that influence the survival of an

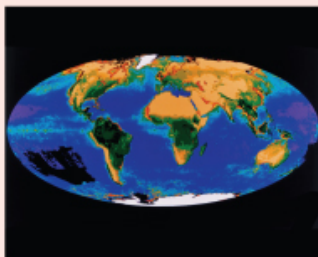
endangered species might use mathematical models to predict how current conservation efforts affect endangered organisms. To produce a sound set of management options, a conservation biologist needs to collect accurate data, including current population size, factors affecting reproduction (like physiology and behavior), habitat requirements (such as plants and soils), and potential human influences on the endangered population and its habitat (which might be derived through studies in sociology and urban ecology). Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap: organism, population, community, and ecosystem ([link]).



Organisms, Populations, and Communities: In a forest, each pine tree is an organism. Together, all the pine trees make up a population. All the plant and animal species in the forest comprise a community.



Ecosystems: This coastal ecosystem in the southeastern United States includes living organisms and the environment in which they live.



The Biosphere: Encompasses all the ecosystems on Earth.

The Karner blue butterfly (*Lycaeides melissa samuelis*) is a rare butterfly that lives only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It can only lay its eggs on lupine plants. (credit: modification of work by J & K Hollingsworth, USFWS) The wild lupine (*Lupinus perennis*) is the host plant for the Karner blue butterfly.

Organismal Ecology

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological, physiological, and behavioral. For instance, the Karner blue butterfly (*Lycaeides melissa samuelis*) ([\[link\]](#)) is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine. This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.



After hatching, the larval caterpillars emerge and spend four to six weeks feeding solely on wild lupine ([\[link\]](#)). The caterpillars pupate (undergo metamorphosis) and emerge as butterflies after

about four weeks. The adult butterflies feed on the nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies' preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).



Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. (Organisms that are all members of the same species are called **conspecifics**.) A population is identified, in part, by where it lives, and its area of population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called **heterospecifics**. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

For example, Karner blue butterfly larvae form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants.

This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the **biotic** components (living things) in an area along with the **abiotic** components (non-living things) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored and how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat. Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, though

the biotic and abiotic portions of the ecosystem.

Career Connection

Ecologist

A career in ecology contributes to many facets of human society. Understanding ecological issues can help society meet the basic human needs of food, shelter, and health care. Ecologists can conduct their research in the laboratory and outside in natural environments ([\[link\]](#)). These natural environments can be as close to home as the stream running through your campus or as far away as the hydrothermal vents at the bottom of the Pacific Ocean. Ecologists manage natural resources such as white-tailed deer populations (*Odocoileus virginianus*) for hunting or aspen (*Populus* spp.) timber stands for paper production. Ecologists also work as educators who teach children and adults at various institutions including universities, high schools, museums, and nature centers. Ecologists may also work in advisory positions assisting local, state, and federal policymakers to develop laws that are ecologically sound, or they may develop those policies and legislation themselves. To become an ecologist requires an undergraduate degree, usually in a natural science. The undergraduate degree is often followed by specialized training or an advanced degree, depending on the area of ecology selected.

Ecologists should also have a broad background in the physical sciences, as well as a sound foundation in mathematics and statistics.

This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study.

(credit: USFWS Mountain Prairie Region, NPS)



Link to Learning



Visit this [site](#) to see Stephen Wing, a marine ecologist from the University of Otago, discuss the

role of an ecologist and the types of issues ecologists explore.

Section Summary

Ecology is the study of the interactions of living things with their environment. Ecologists ask questions across four levels of biological organization—organismal, population, community, and ecosystem. At the organismal level, ecologists study individual organisms and how they interact with their environments. At the population and community levels, ecologists explore, respectively, how a population of organisms changes over time and the ways in which that population interacts with other species in the community. Ecologists studying an ecosystem examine the living species (the biotic components) of the ecosystem as well as the nonliving portions (the abiotic components), such as air, water, and soil, of the environment.

Review Questions

Which of the following is a biotic factor?

1. wind
 2. disease-causing microbe
 3. temperature
 4. soil particle size
-

B

The study of nutrient cycling through the environment is an example of which of the following?

1. organismal ecology
 2. population ecology
 3. community ecology
 4. ecosystem ecology
-

D

Free Response

Ecologists often collaborate with other researchers interested in ecological questions. Describe the levels of ecology that would be easier for collaboration because of the similarities of questions asked. What levels of

ecology might be more difficult for collaboration?

Ecologists working in organismal or population ecology might ask similar questions about how the biotic and abiotic conditions affect particular organisms and, thus, might find collaboration to be mutually beneficial. Levels of ecology such as community ecology or ecosystem ecology might pose greater challenges for collaboration because these areas are very broad and may include many different environmental components.

The population is an important unit in ecology as well as other biological sciences. How is a population defined, and what are the strengths and weaknesses of this definition? Are there some species that at certain times or places are not in populations?

It is beneficial to consider a population to be all of the individuals living in the same area at the same time because it allows the ecologist to identify and study all of the abiotic and biotic factors that may affect the members of the population. However, this definition of a population could be considered a drawback if it prohibits the ecologist from studying a

population's individuals that may be transitory, but still influential. Some species with members that have a wide geographic range might not be considered to be a population, but could still have many of the qualities of a population.

Glossary

abiotic

nonliving components of the environment

biotic

living components of the environment

conspecifics

individuals that are members of the same species

ecology

study of interaction between living things and their environment

heterospecifics

individuals that are members of different species

Biogeography

By the end of this section, you will be able to:

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the affect of abiotic factors on net primary productivity

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of **biomes**: large areas of land with similar climate, flora, and fauna.

Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal. (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome) Listed as federally

endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens. (credit: Forest & Kim Starr) The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham) Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths. The mature cones of the jack pine (*Pinus banksiana*) open only when exposed to high temperatures, such as during a forest fire. A fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. (credit: USDA)

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant

communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine

patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic** species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia ([link](#)ab).



(a)



(b)

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Link to Learning



Check out this [video](#) to observe a platypus swimming in its natural habitat in New South

Wales, Australia.

Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist ([\[link\]](#)).



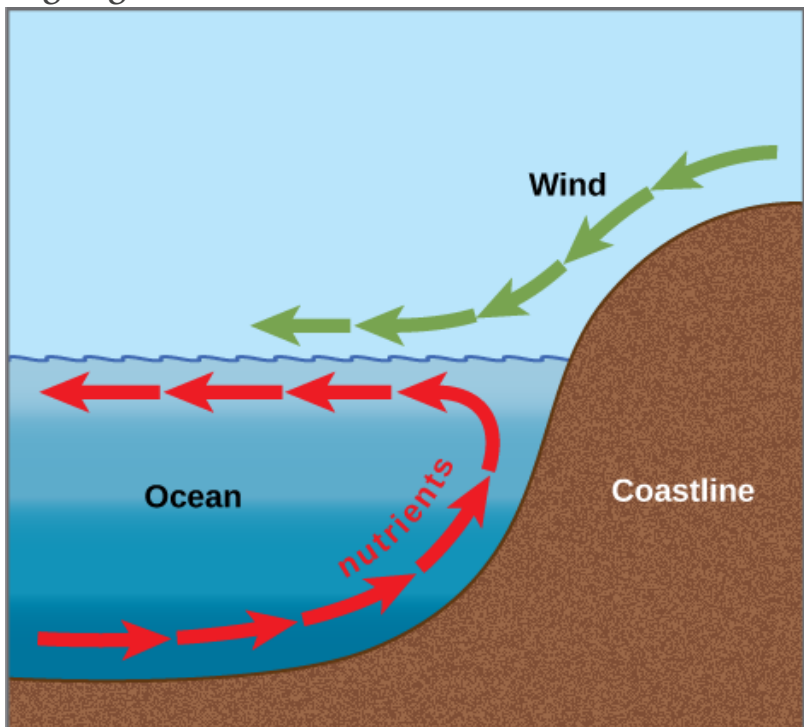
Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty ([\[link\]](#)). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.



In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. **Ocean upwelling** is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline ([\[link\]](#)). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

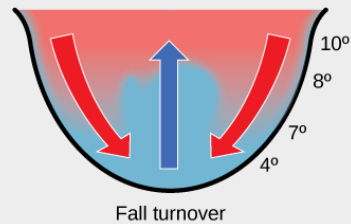
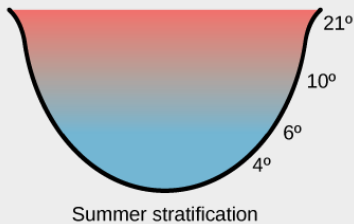
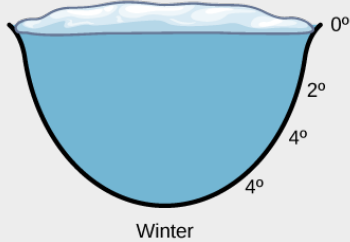


In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The **spring and fall turnover** is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water ([\[link\]](#)). These turnovers are caused by the formation of a **thermocline**: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

Art Connection

The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and

denser water sinks.



How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature

of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface ([\[link\]](#)). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

Temperature

Temperature affects the physiology of living things as well as the density and state of water.

Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures.

Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are adapted to surviving in extremely

hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows

animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water

with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important

in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine—a coniferous tree—requires heat from fire for its seed cones to open ([\[link\]](#)). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.



Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). **Net primary productivity** is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the **aboveground biomass** per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when

considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment.

Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO₂) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Section Summary

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Endemic species are species that are naturally found only in a specific geographic area. The distribution of living things is

influenced by several environmental factors that are, in part, controlled by the latitude or elevation at which an organism is found. Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients and other abiotic factors important in aquatic ecosystems. Energy sources, temperature, water, inorganic nutrients, and soil are factors limiting the distribution of living things in terrestrial systems. Net primary productivity is a measure of the amount of biomass produced by a biome.

Art Connections

[\[link\]](#) How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

[\[link\]](#) Tropical lakes don't freeze, so they don't undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

Review Questions

Understory plants in a temperate forest have adaptations to capture limited ____.

1. water
2. nutrients
3. heat
4. sunlight

D

An ecologist hiking up a mountain may notice different biomes along the way due to changes in all of the following except:

1. elevation
2. rainfall
3. latitude
4. temperature

C

Free Response

Compare and contrast ocean upwelling and spring and fall turnovers.

Ocean upwelling is a continual process that occurs year-round. Spring and fall turnover in freshwater lakes and ponds, however, is a seasonal process that occurs due to temperature changes in the water that take place during springtime warming and autumn cooling. Both ocean upwelling and spring and fall turnover enable nutrients in the organic materials at the bottom of the body of water to be recycled and reused by living things.

Many endemic species are found in areas that are geographically isolated. Suggest a plausible scientific explanation for why this is so.

Areas that have been geographically isolated for very long periods of time allow unique species to evolve; these species are distinctly different from those of surrounding areas and remain so, since geographic isolation keeps them separated from other species.

Glossary

aboveground biomass

total mass of aboveground living plants per area

biogeography

study of the geographic distribution of living things and the abiotic factors that affect their distribution

biome

ecological community of plants, animals, and other organisms that is adapted to a characteristic set of environmental conditions

endemic

species found only in a specific geographic area that is usually restricted in size

fall and spring turnover

seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top

net primary productivity

measurement of the energy accumulation within an ecosystem, calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration

ocean upwelling

rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline

thermocline

layer of water with a temperature that is significantly different from that of the surrounding layers

Climate and the Effects of Global Climate Change

By the end of this section, you will be able to:

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. **Global climate change** is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global

climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, **weather** refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered “average” weather.

Ice at the Russian Vostok station in East Antarctica was laid down over the course 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO₂ trapped in the ice, scientists have determined past atmospheric CO₂ concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present. The atmospheric concentration of CO₂ has risen steadily since the beginning of industrialization. The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: "Pöllö"/Wikimedia Commons)

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

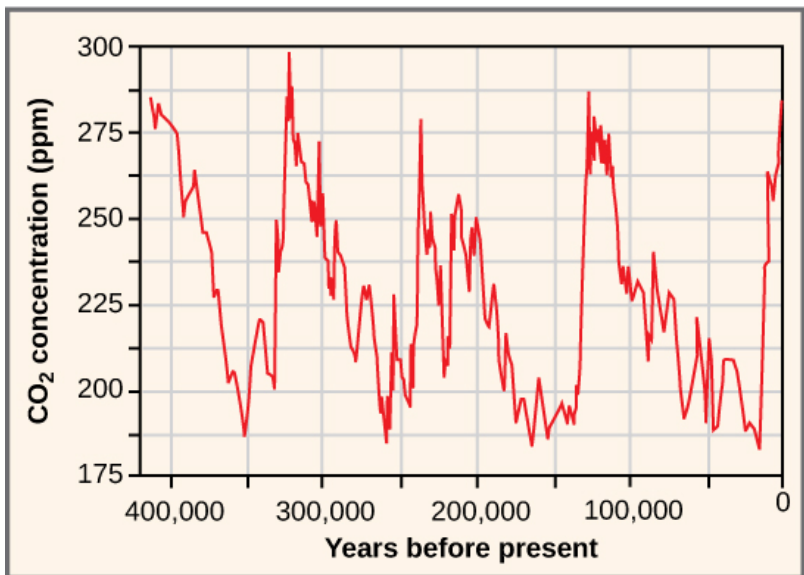
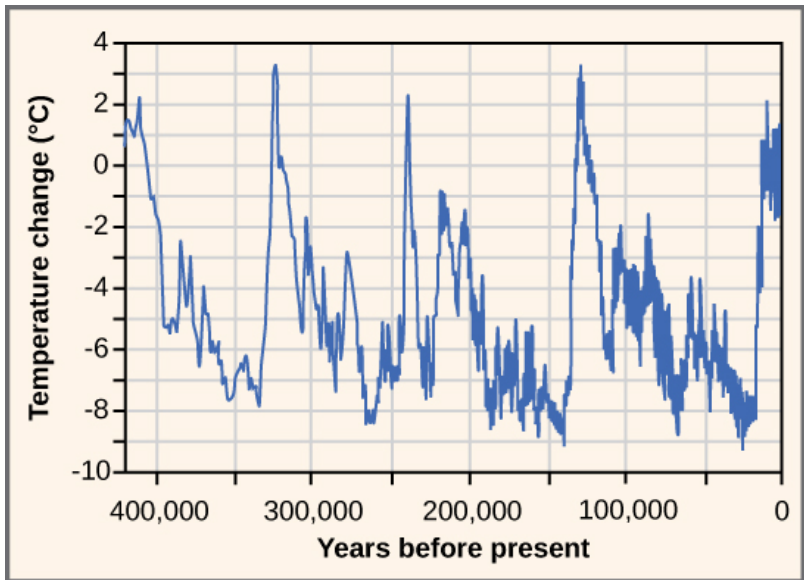
Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years ([link](#)a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0 °C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the

graph in [\[link\]](#)**b** shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. [\[link\]](#)**b** shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.



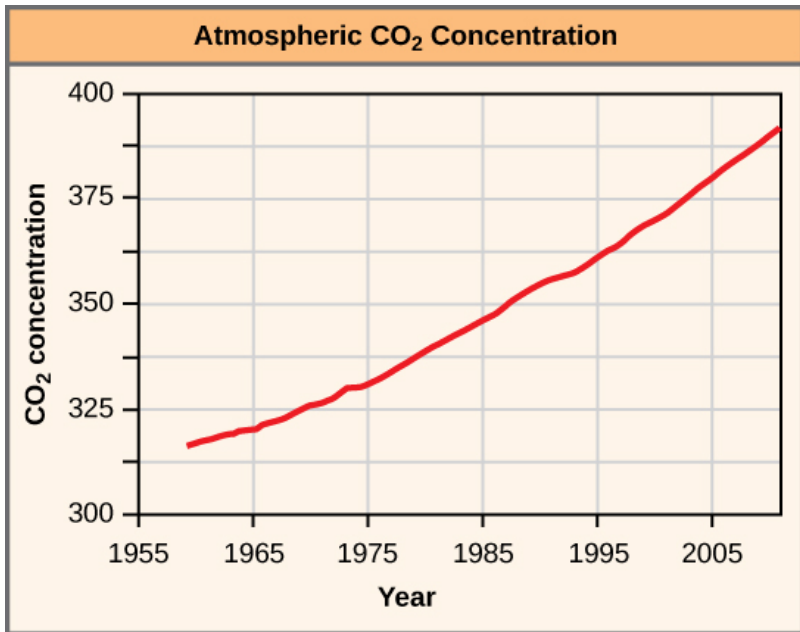
[\[link\]](#) a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the

temperature change that has occurred in the more recent past. Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of

human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise ([link](#)).



Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly

observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The **Milankovitch cycles** describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. **Solar intensity** is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to **haze-effect cooling**, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as **greenhouse gases** trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's

surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the **greenhouse effect**: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration.

However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas ([\[link\]](#)). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates.

Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth's geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent

of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this [NASA video](#) to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may

be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier ([\[link\]](#)) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km³ of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and

sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Section Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was

a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

Review Questions

Which of the following is an example of a weather event?

1. The hurricane season lasts from June 1

- through November 30.
2. The amount of atmospheric CO₂ has steadily increased during the last century.
 3. A windstorm blew down trees in the Boundary Waters Canoe Area in Minnesota on July 4, 1999.
 4. Deserts are generally dry ecosystems having very little rainfall.
-

C

Which of the following natural forces is responsible for the release of carbon dioxide and other atmospheric gases?

1. the Milankovitch cycles
 2. volcanoes
 3. solar intensity
 4. burning of fossil fuels
-

B

Free Response

Compare and contrast how natural- and human-

induced processes have influenced global climate change.

Natural processes such as the Milankovitch cycles, variation in solar intensity, and volcanic eruptions can cause periodic, intermittent changes in global climate. Human activity, in the form of emissions from the burning of fossil fuels, has caused a progressive rise in the levels of atmospheric carbon dioxide.

Predict possible consequences if carbon emissions from fossil fuels continue to rise.

If carbon emissions continue to rise, the global temperature will continue to rise; thus, ocean waters will cause the rising of sea levels at the coastlines. Continued melting of glaciers and reduced spring and summer meltwaters may cause summertime water shortages. Changes in seasonal temperatures may alter lifecycles and interrupt breeding patterns in many species of plants and animals.

Glossary

clathrates

frozen chunks of ice and methane found at

the bottom of the ocean

climate

long-term, predictable atmospheric conditions
present in a specific area

global climate change

altered global weather patterns, including a
worldwide increase in temperature, due
largely to rising levels of atmospheric carbon
dioxide

greenhouse effect

warming of Earth due to carbon dioxide and
other greenhouse gases in the atmosphere

greenhouse gases

atmospheric gases such as carbon dioxide and
methane that absorb and emit radiation, thus
trapping heat in Earth's atmosphere

haze-effect cooling

effect of the gases and solids from a volcanic
eruption on global climate

Milankovitch cycles

cyclic changes in the Earth's orbit that may
affect climate

solar intensity

amount of solar power energy the sun emits
in a given amount of time

weather

conditions of the atmosphere during a short
period of time

Terrestrial Biomes

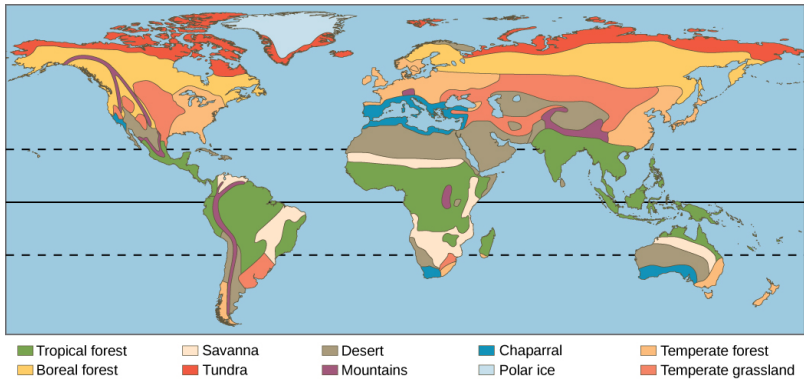
By the end of this section, you will be able to:

- Identify the two major abiotic factors that determine the type of terrestrial biome in an area
- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

Earth's biomes can be either terrestrial or aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Annual totals and fluctuations of precipitation affect the kinds of vegetation and animal life that can exist in broad geographical regions. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of a biome. Since a biome is defined by climate, the same biome can occur in geographically distinct areas with similar climates ([\[link\]](#)). There are also large areas on Antarctica, Greenland, and in mountain ranges that are covered by permanent glaciers and support very little life. Strictly speaking, these are not considered biomes and in addition to extremes of cold, they are also often deserts with very low precipitation.

Each of the world's eight major biomes is distinguished by characteristic temperatures and

amount of precipitation. Polar ice caps and mountains are also shown.



Species diversity is very high in tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River. (credit: Roosevelt Garcia)

Tropical Forest

Tropical rainforests are also referred to as tropical wet forests. This biome is found in equatorial regions ([\[link\]](#)). Tropical rainforests are the most diverse terrestrial biome. This biodiversity is still largely unknown to science and is under extraordinary threat primarily through logging and deforestation for agriculture. Tropical rainforests have also been described as nature's pharmacy because of the potential for new drugs that is largely hidden in the chemicals produced by the huge diversity of plants, animals, and other organisms. The vegetation is characterized by plants with spreading roots and broad leaves that fall off throughout the year, unlike the trees of deciduous

forests that lose their leaves in one season. These forests are “evergreen,” year-round.

The temperature and sunlight profiles of tropical rainforests are stable in comparison to that of other terrestrial biomes, with average temperatures ranging from 20°C to 34°C (68°F to 93°F). Month-to-month temperatures are relatively constant in tropical rainforests, in contrast to forests further from the equator. This lack of temperature seasonality leads to year-round plant growth, rather than the seasonal growth seen in other biomes. In contrast to other ecosystems, a more constant daily amount of sunlight (11–12 hours per day) provides more solar radiation, thereby a longer period of time for plant growth.

The annual rainfall in tropical rainforests ranges from 250 cm to more than 450 cm (8.2–14.8 ft) with considerable seasonal variation. Tropical rainforests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical rainforest can still exceed the *annual* rainfall of some other biomes, such as deserts.

Tropical rainforests have high net primary productivity because the annual temperatures and precipitation values support rapid plant growth ([\[link\]](#)). However, the high rainfall quickly leaches

nutrients from the soils of these forests, which are typically low in nutrients. Tropical rainforests are characterized by vertical layering of vegetation and the formation of distinct habitats for animals within each layer. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short, shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper **canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, animals, and other organisms within the tropical wet forests. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground rarely ever descending to the forest floor.

Rainforests are not the only forest biome in the tropics; there are also tropical dry forests, which are characterized by a dry season of varying lengths. These forests commonly experience leaf loss during the dry season to one degree or another. The loss of leaves from taller trees during the dry season opens up the canopy and allows sunlight to the forest floor that allows the growth of thick ground-level brush, which is absent in tropical rainforests. Extensive tropical dry forests occur in Africa (including Madagascar), India, southern Mexico, and South America.



Although savannas are dominated by grasses, small woodlands, such as this one in Mount Archer National Park in Queensland, Australia, may dot the landscape. (credit: "Ethel Aardvark"/Wikimedia Commons)

Savannas

Savannas are grasslands with scattered trees, and they are found in Africa, South America, and northern Australia ([\[link\]](#)). Savannas are hot, tropical areas with temperatures averaging from 24°C –29°C (75°F –84°F) and an annual rainfall of 51–127 cm (20–50 in). Savannas have an extensive dry season and consequent fires. As a result, scattered in the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there

are relatively few trees ([\[link\]](#)). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Many desert plants have tiny leaves or no leaves at all to reduce water loss. The leaves of ocotillo, shown here in the Chihuahuan Desert in Big Bend National Park, Texas, appear only after rainfall and then are shed. (credit “bare ocotillo”: "Leaflet"/ Wikimedia Commons)

Deserts

Subtropical deserts exist between 15° and 30° north and south latitude and are centered on the Tropic of Cancer and the Tropic of Capricorn ([\[link\]](#)). Deserts are frequently located on the

downwind or lee side of mountain ranges, which create a rain shadow after prevailing winds drop their water content on the mountains. This is typical of the North American deserts, such as the Mohave and Sonoran deserts. Deserts in other regions, such as the Sahara Desert in northern Africa or the Namib Desert in southwestern Africa are dry because of the high-pressure, dry air descending at those latitudes. Subtropical deserts are very dry; evaporation typically exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60°C (140°F) and nighttime temperatures approaching 0°C (32°F). The temperature drops so far because there is little water vapor in the air to prevent radiative cooling of the land surface. Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. Some years may receive tiny amounts of rainfall, while others receive more. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The low species diversity of this biome is closely related to its low and unpredictable precipitation. Despite the relatively low diversity, desert species exhibit fascinating adaptations to the harshness of their environment. Very dry deserts lack perennial vegetation that lives from one year to the next;

instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Perennial plants in deserts are characterized by adaptations that conserve water: deep roots, reduced foliage, and water-storing stems ([\[link\]](#)). Seed plants in the desert produce seeds that can lie dormant for extended periods between rains. Most animal life in subtropical deserts has adapted to a nocturnal life, spending the hot daytime hours beneath the ground. The Namib Desert is the oldest on the planet, and has probably been dry for more than 55 million years. It supports a number of endemic species (species found only there) because of this great age. For example, the unusual gymnosperm *Welwitschia mirabilis* is the only extant species of an entire order of plants. There are also five species of reptiles considered endemic to the Namib.

In addition to subtropical deserts there are cold deserts that experience freezing temperatures during the winter and any precipitation is in the form of snowfall. The largest of these deserts are the Gobi Desert in northern China and southern Mongolia, the Taklimakan Desert in western China, the Turkestan Desert, and the Great Basin Desert of the United States.



The chaparral is dominated by shrubs. (credit: Miguel Vieira)

Chaparral

The **chaparral** is also called scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia ([\[link\]](#)). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in) and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that germinate only after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth. Fire is a natural part of the maintenance of this biome and frequently threatens human habitation in this biome in the U.S. ([\[link\]](#)).



The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA ARS)

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies, and in Eurasia, where they are known as steppes ([\[link\]](#)). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth, which occurs in the spring, summer, and

fall.

Annual precipitation ranges from 25.4 cm to 88.9 cm (10–35 in). Temperate grasslands have few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses. The treeless condition is maintained by low precipitation, frequent fires, and grazing ([\[link\]](#)). The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.



Fires, which are a natural disturbance in temperate grasslands, can be ignited by lightning strikes. It also appears that the lightning-caused fire regime in North American grasslands was enhanced by intentional burning by humans. When fire is

suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand ([\[link\]](#)). This biome is found throughout mid-latitude regions.

Temperatures range between -30°C and 30°C (-22°F to 86°F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall.

Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Deciduous trees are the dominant plant in this biome with fewer evergreen conifers. Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, little photosynthesis occurs during the dormant winter period. Each spring, new leaves appear as temperature increases. Because of the dormant period, the net primary productivity of

temperate forests is less than that of tropical rainforests. In addition, temperate forests show far less diversity of tree species than tropical rainforest biomes.

The trees of the temperate forests leaf out and shade much of the ground; however, more sunlight reaches the ground in this biome than in tropical rainforests because trees in temperate forests do not grow as tall as the trees in tropical rainforests. The soils of the temperate forests are rich in inorganic and organic nutrients compared to tropical rainforests. This is because of the thick layer of leaf litter on forest floors and reduced leaching of nutrients by rainfall. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates and their predators ([\[link\]](#)).



The boreal forest (taiga) has low lying plants and conifer trees. (credit: L.B. Brubaker, NOAA)

Boreal Forests

The **boreal forest**, also known as taiga or coniferous forest, is found roughly between 50° and 60° north latitude across most of Canada, Alaska, Russia, and northern Europe ([\[link\]](#)). Boreal forests are also found above a certain elevation (and below high elevations where trees cannot grow) in mountain ranges throughout the Northern Hemisphere. This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow; little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the Sun is required to warm a needle-like leaf than a broad leaf. Evergreen trees grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles in a nitrogen limiting environment may have had a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate standing biomass over time. Species diversity is less than that seen in temperate forests and tropical rainforests. Boreal forests lack the layered forest structure seen in tropical rainforests or, to a lesser degree, temperate forests. The structure of a boreal forest is often only a tree layer and a ground layer. When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients

are returned to the soil to fuel plant growth ([\[link\]](#)).



Low-growing plants such as shrub willow dominate the tundra landscape during the summer, shown here in the Arctic National Wildlife Refuge. (credit: Arctic National Wildlife Refuge, USFWS)

Arctic Tundra

The **Arctic tundra** lies north of the subarctic boreal forests and is located throughout the Arctic regions of the Northern Hemisphere ([\[link\]](#)). Tundra also exists at elevations above the tree line on mountains. The average winter temperature is -34°C (-29.2°F) and the average summer temperature is 3°C – 12°C (37°F – 52°F). Plants in the Arctic tundra have a short growing season of approximately 50–60 days. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is low (15–

25 cm or 6–10 in) with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation because of the cold temperatures.

Plants in the Arctic tundra are generally low to the ground and include low shrubs, grasses, lichens, and small flowering plants ([\[link\]](#)). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate far into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. The melting of the permafrost in the brief summer provides water for a burst of productivity while temperatures and long days permit it. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Concept in Action



Watch this [Assignment Discovery: Biomes](#) video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Section Summary

Earth has terrestrial and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial biomes: tropical rainforests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and

plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons with cold and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical rainforest, net primary productivity is high as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of water.

Multiple Choice

Which of the following biomes is characterized by abundant water resources?

1. deserts
2. boreal forests
3. savanna
4. tropical wet forests

D

Which of the following biomes is characterized by short growing seasons?

1. deserts

2. tropical wet forests
 3. Arctic tundra
 4. savanna
-

C

Why is the tundra treeless?

1. lack of sufficient water
 2. permanently frozen ground
 3. winters too harsh
 4. too many fires
-

B

Free Response

The extremely low precipitation of subtropical desert biomes might lead one to expect fire to be a major disturbance factor; however, fire is more common in the temperate grassland biome than in the subtropical desert biome. Why is this?

Fire is less common in desert biomes than in

temperate grasslands because deserts have low net primary productivity, thus very little plant biomass to fuel a fire.

In what ways are the subtropical desert and the Arctic tundra similar?

Both the subtropical desert and the Arctic tundra have a low supply of water. In the desert, this is due to extremely low precipitation, and in the Arctic tundra, much of the water is unavailable to plants because it is frozen. Both the subtropical desert and the Arctic tundra have low net primary productivity.

Glossary

arctic tundra

a biome characterized by low average temperatures, brief growing seasons, the presence of permafrost, and limited precipitation largely in the form of snow in which the dominant vegetation are low shrubs, lichens, mosses, and small herbaceous plants

boreal forest

a biome found in temperate and subarctic

regions characterized by short growing seasons and dominated structurally by coniferous trees

canopy

the branches and foliage of trees that form a layer of overhead coverage in a forest

chaparral

a biome found in temperate coastal regions characterized by low trees and dry-adapted shrubs and forbs

permafrost

a perennially frozen portion of the Arctic tundra soil

savanna

a biome located in the tropics with an extended dry season and characterized by a grassland with sparsely distributed trees

subtropical desert

a biome found in the subtropics with hot daily temperatures, very low and unpredictable precipitation, and characterized by a limited dry-adapted vegetation

temperate forest

a biome found in temperate regions with moderate rainfall and dominated structurally by deciduous trees

temperate grassland

a biome dominated by grasses and herbaceous plants due to low precipitation, periodic fires, and grazing

tropical rainforest

a biome found near the equator characterized by stable temperatures with abundant and seasonal rainfall in which trees form the structurally important vegetation

Aquatic Biomes

By the end of this section, you will be able to:

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater biomes

Abiotic Factors Influencing Aquatic Biomes

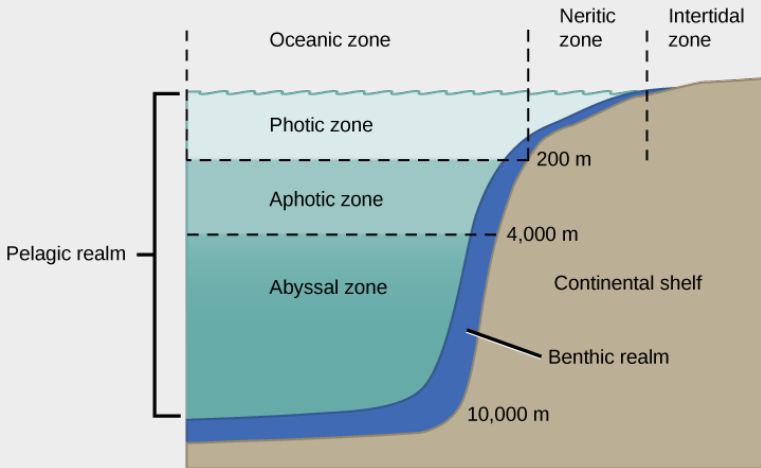
Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water—has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of

organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones ([\[link\]](#)). All of the ocean's open water is referred to as the **pelagic realm** (or zone). The **benthic realm** (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the **photic zone**, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the **aphotic zone**. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

Art Connection

The ocean is divided into different zones based on water depth and distance from the shoreline.



In which of the following regions would you expect to find photosynthetic organisms?

1. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
2. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
3. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
4. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA) Coral reefs are formed by the calcium carbonate skeletons of

coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The **intertidal zone**, which is the zone between high and low tide, is the oceanic region that is closest to land ([\[link\]](#)). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment

because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves ([\[link\]](#)). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.



The **neritic zone** ([\[link\]](#)) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can

penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the **oceanic zone** ([\[link\]](#)). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf

([\[link\]](#)). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the **abyssal zone**, which is at depths of 4000 m or greater. The abyssal zone ([\[link\]](#)) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30° north and south of the equator. The Great Barrier Reef is a well-known reef system located

several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef ([\[link\]](#)). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

Link to Learning



Watch this [National Oceanic and Atmospheric Administration \(NOAA\) video](#) to see marine ecologist Dr. Peter Etnoyer discusses his research on coral organisms.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the **cryptofauna** (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include **predators**, herbivores, or **planktivores**. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.



Evolution Connection

Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners

evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching.

When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go

unchecked.

Although a rise in global temperatures of 1–2°C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary.

Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton) Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret

walks among cypress trees. (credit: NPS)

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as **ecosystem services**. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers

and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an **algal bloom**. Algal blooms ([link](#)) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.



Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as **source water**. The source water is usually cold, low in nutrients, and clear. The **channel** (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point

of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into

the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. **Emergent vegetation** consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes ([\[link\]](#)). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net

primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Section Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

Art Connections

[\[link\]](#) In which of the following regions would you expect to find photosynthetic organisms?

1. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
2. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
3. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
4. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

[\[link\]](#) C. Photosynthetic organisms would be found in the photic, abyssal, neritic, and oceanic zones.

Review Questions

Where would you expect to find the most photosynthesis in an ocean biome?

1. aphotic zone
2. abyssal zone
3. benthic realm

4. intertidal zone

D

A key feature of estuaries is:

1. low light conditions and high productivity
 2. salt water and fresh water
 3. frequent algal blooms
 4. little or no vegetation
-

B

Free Response

Scientists have discovered the bodies of humans and other living things buried in bogs for hundreds of years, but not yet decomposed. Suggest a possible biological explanation for why such bodies are so well-preserved.

Bogs are low in oxygen and high in organic acids. The low oxygen content and the low pH both slow the rate of decomposition.

Describe the conditions and challenges facing organisms living in the intertidal zone.

Organisms living in the intertidal zone must tolerate periodic exposure to air and sunlight and must be able to be periodically dry. They also must be able to endure the pounding waves; for this reason, some shoreline organisms have hard exoskeletons that provide protection while also reducing the likelihood of drying out.

Glossary

abyssal zone

deepest part of the ocean at depths of 4000 m or greater

algal bloom

rapid increase of algae in an aquatic system

aphotic zone

part of the ocean where no light penetrates

benthic realm

(also, benthic zone) part of the ocean that extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor

channel

width of a river or stream from one bank to the other bank

coral reef

ocean ridges formed by marine invertebrates living in warm, shallow waters within the photic zone

cryptofauna

invertebrates found within the calcium carbonate substrate of coral reefs

ecosystem services

human benefits and services provided by natural ecosystems

emergent vegetation

wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface

estuary

biomes where a source of fresh water, such as a river, meets the ocean

intertidal zone

part of the ocean that is closest to land; parts extend above the water at low tide

neritic zone

part of the ocean that extends from low tide

to the edge of the continental shelf

oceanic zone

part of the ocean that begins offshore where the water measures 200 m deep or deeper

pelagic realm

(also, pelagic zone) open ocean waters that are not close to the bottom or near the shore

photic zone

portion of the ocean that light can penetrate

planktivore

animal species that eats plankton

predator

animal species that hunt and are carnivores or “flesh eaters”

Sargassum

type of free-floating marine seaweed

source water

point of origin of a river or stream

Population Demography

By the end of this section, you will be able to:

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, **demography**, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, **life tables**, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is commonly used when discussing humans, all living populations can be studied using this approach.

A scientist uses a quadrat to measure population

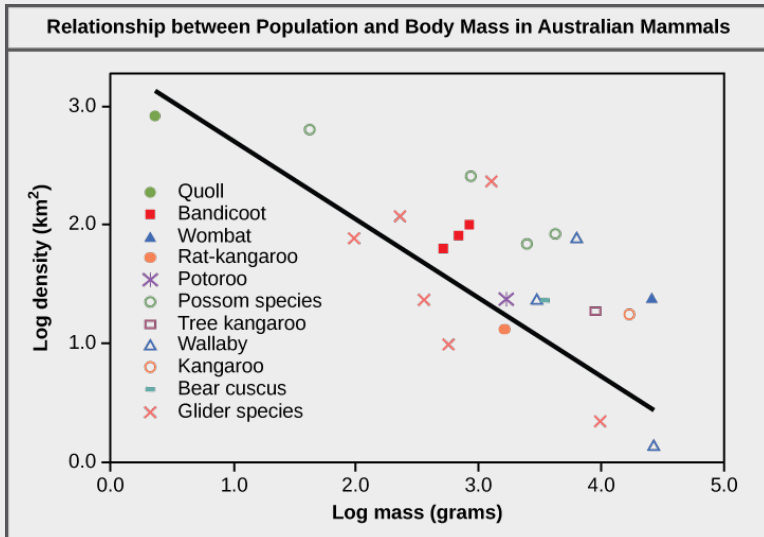
size and density. (credit: NPS Sonoran Desert Network) Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar)

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its **population size (N)**, the total number of individuals, and its **population density**, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. As is shown in [\[link\]](#), smaller organisms tend to be more densely distributed than larger organisms.

Art Connection

Australian mammals show a typical inverse relationship between population density and body size.

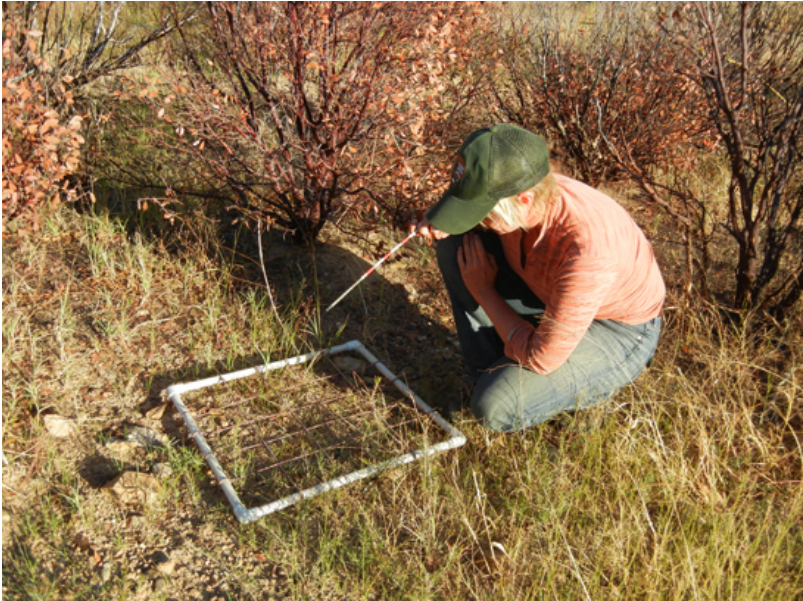


As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Population Research Methods

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this

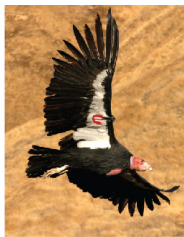
data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a **quadrat** may be used ([\[link\]](#)). A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m² quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m² might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.



For mobile organisms, such as mammals, birds, or fish, a technique called **mark and recapture** is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked ([\[link\]](#)).



(a)



(b)



(c)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can determine the population size (N) using the following equation:

$$\frac{\text{number marked first catch} \times \text{total number of second catch}}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.

$$(80 \times 100) / 20 = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

There are some limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, animals may preferentially be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing

their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

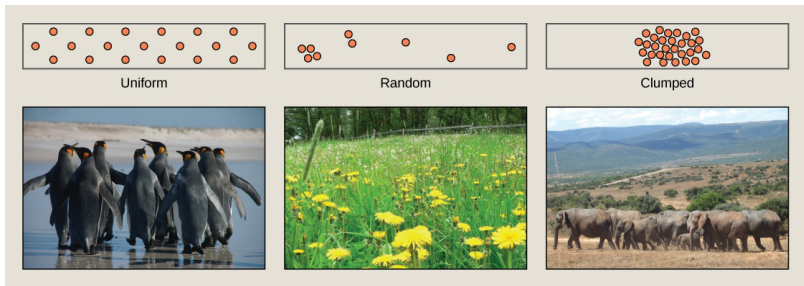
Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals.

Species dispersion patterns (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, dispersed randomly with no

predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns, respectively ([\[link\]](#)). Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla*, a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.



Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate

because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or age structure (the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. Life expectancy is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. Life tables divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by

the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their **mortality rate**), the percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval. An example of a life table is shown in [\[link\]](#) from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \times 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} \times 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it

could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in column E.

**Life Table
of Dall
Mountain
Sheep [\[footnote\]](#) Data
Adapted
from
Edward
S.
Deevey,
Jr., “Life
Tables
for
Natural
Populations
of
Animals,”
*The
Quarterly
Review of
Biology*
22, no. 4
(December
1947):**

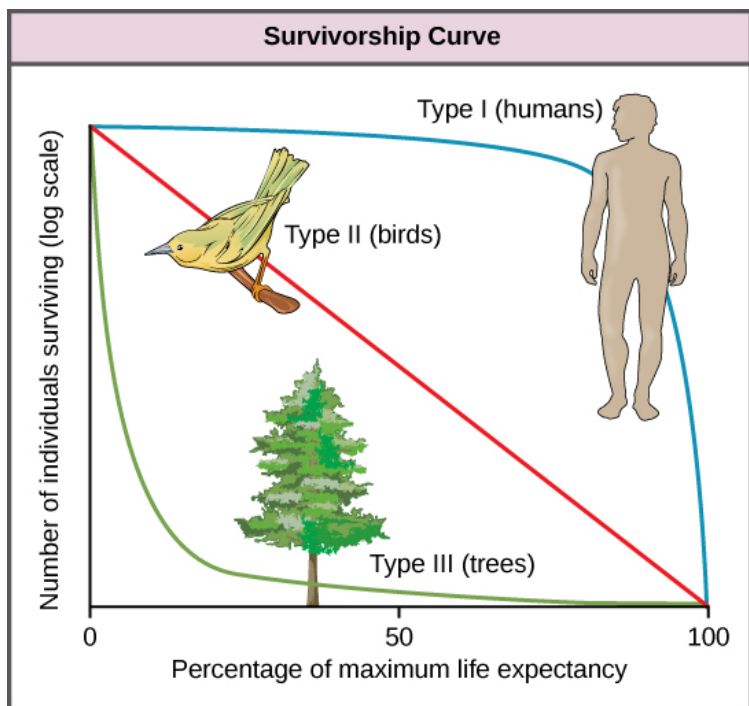
233-314.

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0-0.5	54	1000	54.0	7.06
0.5-1	145	946	153.3	
1-2	12	801	15.0	7.7
2-3	13	789	16.5	6.9
3-4	12	776	15.5	5.9
4-5	30	764	39.3	5.0
5-6	46	724	62.7	4.2
6-7	48	689	69.8	3.4
7-8	69	640	107.8	2.6
8-9	132	571	231.2	1.9
9-10	187	439	426.0	1.3
10-11	156	252	619.0	0.9
11-12	90	96	937.5	0.6
12-13	3	6	500.0	1.2
13-14	3	3	1000	0.7

This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

Survivorship Curves

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations ([\[link\]](#)). Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or Type II survivorship curve because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are “on their own” and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.



Section Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, dispersion pattern, age structure, and sex ratio. Life tables are useful to calculate life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

Art Connections

[\[link\]](#) As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

[\[link\]](#) Smaller animals require less food and other resources, so the environment can support more of them.

Review Questions

Which of the following methods will tell an ecologist about both the size and density of a population?

1. mark and recapture
2. mark and release
3. quadrat
4. life table

C

Which of the following is best at showing the

life expectancy of an individual within a population?

1. quadrat
2. mark and recapture
3. survivorship curve
4. life table

D

Humans have which type of survivorship curve?

1. Type I
2. Type II
3. Type III
4. Type IV

A

Free Response

Describe how a researcher would determine the size of a penguin population in Antarctica using the mark and release method.

The researcher would mark a certain number of penguins with a tag, release them back into the population, and, at a later time, recapture penguins to see what percentage of the recaptured penguins was tagged. This percentage would allow an estimation of the size of the penguin population.

Glossary

demography

statistical study of changes in populations over time

life table

table showing the life expectancy of a population member based on its age

mark and recapture

technique used to determine population size in mobile organisms

mortality rate

proportion of population surviving to the beginning of an age interval that die during the age interval

population density

number of population members divided by the area or volume being measured

population size (N)

number of population members in a habitat at the same time

quadrat

square made of various materials used to determine population size and density in slow moving or stationary organisms

species dispersion pattern

(also, species distribution pattern) spatial location of individuals of a given species within a habitat at a particular point in time

survivorship curve

graph of the number of surviving population members versus the relative age of the member

Life Histories and Natural Selection

By the end of this section, you will be able to:

- Describe how life history patterns are influenced by natural selection
- Explain different life history patterns and how different reproductive strategies affect species' survival

A species' **life history** describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species' life history is genetically determined and shaped by the environment and natural selection.

The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by “Shiny Things”/ Flickr)

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in

determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an **energy budget**: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age.

This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds

or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health.

Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish like guppies use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species “blow it all” and use up most of their energy reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. **Semelparity** occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon ([link](#)), which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook's post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle ("heat"): a hormonally induced physiological condition preparing the body for

successful mating ([link](#)b). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation ([link](#)c).



Link to Learning



Play this [interactive PBS evolution-based mating game](#) to learn more about reproductive strategies.

Evolution Connection

Energy Budgets, Reproductive Costs, and Sexual Selection in *Drosophila*

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females

had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings ([\[link\]](#)).^[footnote] Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed “resource-depleted,” while males that had not mated were termed “non-resource-depleted.”

The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

Adapted from Phillip G. Byrne and William R. Rice, "Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*," Proc Biol Sci. 273, no. 1589 (2006): 917-922, doi: 10.1098/rspb.2005.3372. Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's lifespan, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

Section Summary

All species have evolved a pattern of living, called a life history strategy, in which they partition energy for growth, maintenance, and reproduction. These patterns evolve through natural selection; they allow species to adapt to their environment to obtain the resources they need to successfully reproduce. There is an inverse relationship between fecundity and parental care. A species may reproduce early in life to ensure surviving to a reproductive age or reproduce later in life to become larger and healthier and better able to give parental care. A species may reproduce once (semelparity) or many times (iteroparity) in its life.

Review Questions

Which of the following is associated with long-term parental care?

1. few offspring
2. many offspring
3. semelparity
4. fecundity

A

Which of the following is associated with multiple reproductive episodes during a species' lifetime?

1. semiparity
2. iteroparity
3. semelparity
4. fecundity

B

Which of the following is associated with the reproductive potential of a species?

1. few offspring
2. many offspring
3. semelparity
4. fecundity

D

Free Response

Why is long-term parental care not associated with having many offspring during a reproductive episode?

Parental care is not feasible for organisms having many offspring because they do not have the energy available to take care of offspring. Most of their energy budget is used in the formation of seeds or offspring, so there is little left for parental care. Also, the sheer number of offspring would make individual parental care impossible.

Glossary

energy budget

allocation of energy resources for body maintenance, reproduction, and parental care

fecundity

potential reproductive capacity of an individual

iteroparity

life history strategy characterized by multiple reproductive events during the lifetime of a species

life history

inherited pattern of resource allocation under

the influence of natural selection and other evolutionary forces

semelparity

life history strategy characterized by a single reproductive event followed by death

Environmental Limits to Population Growth

By the end of this section, you will be able to:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain models that have been accepted for decades are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped

curve.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called **exponential growth**.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is that the **population growth rate**—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the

population would have increased from 1000 to more than 16 billion. When the population size, N , is plotted over time, a **J-shaped growth curve** is produced ([link](#)).

The bacteria example is not representative of the real world where resources are limited.

Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate (D)** (number organisms that die during a particular time interval) is subtracted from the **birth rate (B)** (number organisms that are born during that interval). This is shown in the following formula:

$$\begin{aligned} \Delta N \text{ (change in number)} / \Delta T \text{ (change in time)} \\ = B \text{ (birth rate)} - D \text{ (death rate)} \end{aligned}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, B (birth rate) = bN (the per capita birth rate “ b ” multiplied by the number of individuals “ N ”) and D (death rate) = dN (the per capita death rate “ d ” multiplied by the number of individuals “ N ”). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the “instantaneous” growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

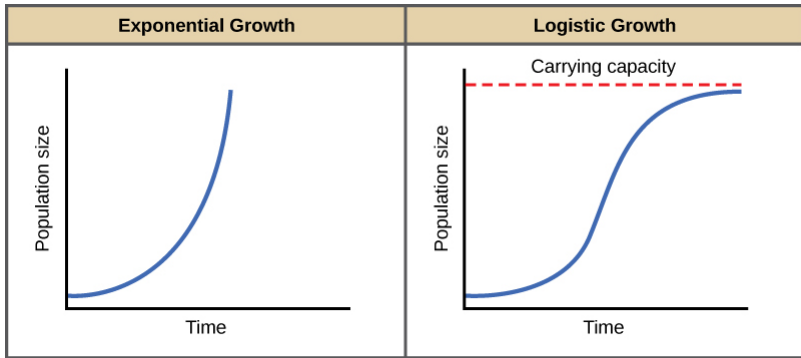
$$dN / dT = bN - dN = (b - d)N$$

Notice that the “ d ” associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called “ d .” The difference between birth and death rates is further simplified by substituting the term “ r ” (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value “ r ” can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population’s size is unchanging, a condition known as **zero population growth**. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its **biotic potential, or r_{max}** , thus changing the equation to:

$$\frac{dN}{dT} = r_{max} N$$



Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the “struggle for existence,” which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments

where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off ([\[link\]](#)). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity, or K** .

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression “ $K - N$ ” is indicative of how many individuals may be added to a population at a given stage, and “ $K - N$ ” divided by “ K ” is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\frac{dN}{dt} = r \max \frac{dN}{dt} = r \max N \frac{(K - N)}{K}$$

Notice that when N is very small, $(K-N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{\max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K-N)/K$ come close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K . This model also allows for the population of a negative population growth, or a population decline. This

occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K-N)/K$ is negative).

A graph of this equation yields an **S-shaped curve** ([\[link\]](#)), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition**

(intra- = “within”; -specific = “species”).

Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment’s carrying capacity.

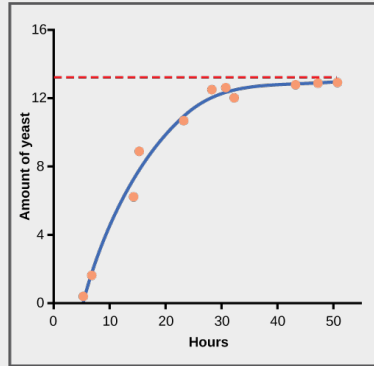
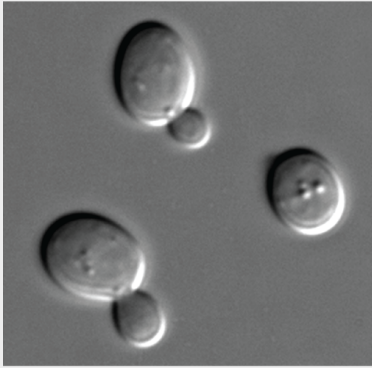
Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube ([link](#)a). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals ([link](#)b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

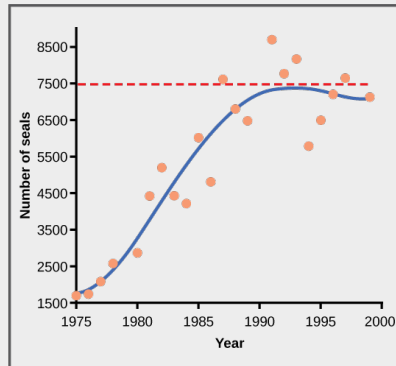
Art Connection

(a) Yeast grown in ideal conditions in a test tube

show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.



(a)



(b)

If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.
2. The carrying capacity of seals would decrease, but the seal population would remain the same.
3. The number of seal deaths would increase but

the number of births would also increase, so the population size would remain the same.

4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Section Summary

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment.

Art Connections

[\[link\]](#) **b** If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.
2. The carrying capacity of seals would

decrease, but the seal population would remain the same.

3. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

[\[link\]](#) b A

Review Questions

Species with limited resources usually exhibit a(n) _____ growth curve.

1. logistic
2. logical
3. experimental
4. exponential

A

The maximum rate of increased characteristic

of a species is called its _____.

1. limit
2. carrying capacity
3. biotic potential
4. exponential growth pattern

C

The population size of a species capable of being supported by the environment is called its _____.

1. limit
2. carrying capacity
3. biotic potential
4. logistic growth pattern

B

Free Response

Describe the rate of population growth that would be expected at various parts of the S-shaped curve of logistic growth.

In the first part of the curve, when few individuals of the species are present and resources are plentiful, growth is exponential, similar to a J-shaped curve. Later, growth slows due to the species using up resources. Finally, the population levels off at the carrying capacity of the environment, and it is relatively stable over time.

Glossary

biotic potential (r_{\max})

maximal potential growth rate of a species

birth rate (B)

number of births within a population at a specific point in time

carrying capacity (K)

number of individuals of a species that can be supported by the limited resources of a habitat

death rate (D)

number of deaths within a population at a specific point in time

exponential growth

accelerating growth pattern seen in species under conditions where resources are not

limiting

intraspecific competition

competition between members of the same species

J-shaped growth curve

shape of an exponential growth curve

logistic growth

leveling off of exponential growth due to limiting resources

population growth rate

number of organisms added in each reproductive generation

S-shaped growth curve

shape of a logistic growth curve

zero population growth

steady population size where birth rates and death rates are equal

Population Dynamics and Regulation

By the end of this section, you will be able to:

- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in **interspecific competition**: that is, they share the environment with other species, competing with them for the same resources. These factors are also important to

understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197,

doi:10.1016/0035-9203(82)90272-3. Martin Walker et al., "Density-Dependent Effects on the Weight of Female *Ascaris lumbricoides* Infections of Humans and its Impact on Patterns of Egg Production."

Parasites & Vectors 2, no. 11 (February 2009),

doi:10.1186/1756-3305-2-11. In this population of roundworms, fecundity (number of eggs) decreases with population density. [footnote]

N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran."

Transactions of the Royal Society of Tropical Medicine and Hygiene 76, no. 2 (1982): 187-197,

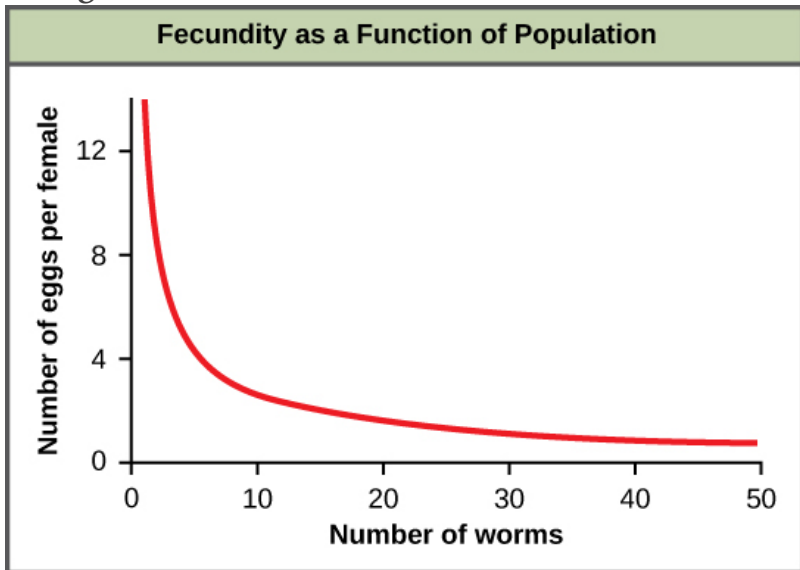
Density-dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites.

Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in [\[link\]](#) with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals.[\[footnote\]](#) Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence.[\[footnote\]](#) The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further

investigation.



Density-independent Regulation and Interaction with Density-dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very

complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Evolution Connection

Why Did the Woolly Mammoth Go Extinct?

The three photos include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world, from the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by “Tanapon”/Flickr; credit c: modification of work by Matt Howry)





It's easy to get lost in the discussion of dinosaurs and theories about why they went extinct 65 million years ago. Was it due to a meteor slamming into Earth near the coast of modern-day Mexico, or was it from some long-term weather cycle that is not yet understood? One hypothesis that will never be proposed is that humans had something to do with it. Mammals were small, insignificant creatures of the forest 65 million years ago, and no humans existed.

Woolly mammoths, however, began to go extinct about 10,000 years ago, when they shared the Earth with humans who were no different anatomically than humans today ([\[link\]](#)).

Mammoths survived in isolated island populations as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other regions of the north. Scientists have sequenced at least 50 percent of its genome and believe mammoths are between 98 and 99

percent identical to modern elephants.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.^[footnote] It is also well documented that humans hunted these animals. A 2012 study showed that no single factor was exclusively responsible for the extinction of these magnificent creatures.^[footnote] In addition to human hunting, climate change, and reduction of habitat, these scientists demonstrated another important factor in the mammoth's extinction was the migration of humans across the Bering Strait to North America during the last ice age 20,000 years ago.

David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079.G.M.

MacDonald et al., "Pattern of Extinction of the Woolly Mammoth in Beringia." *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. Once we contributed to a species' decline using primitive hunting technology only.

(a) Elephants are considered K -selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K -selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r -selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

Life Histories of K -selected and r -selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of K -selected versus r -selected species.

Early Theories about Life History: K -selected and r -selected Species

By the second half of the twentieth century, the concept of K - and r -selected species was used extensively and successfully to study populations. The concept relates not only reproductive strategies, but also to a species' habitat and behavior, especially in the way that they obtain resources and

care for their young. It includes length of life and survivorship factors as well. For this analysis, population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although they are really two ends of a continuum.

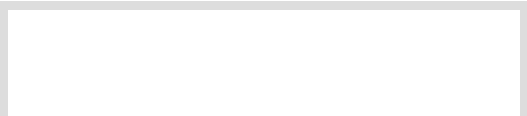
***K*-selected species** are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, a long gestation period, and often give long-term care to their offspring (Table B45_04_01). While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of *K*-selected species are primates including humans), elephants, and plants such as oak trees ([link](#)a).

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these

years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).

In contrast, ***r*-selected species** have a large number of small offspring (hence their *r* designation ([\[link\]](#)). This strategy is often employed in unpredictable or changing environments. Animals that are *r*-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of *r*-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion ([\[link\]](#)**b**). Dandelions have small seeds that are wind dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.



Characteristics of K -selected and r -selected species

Characteristics of K -selected species

Mature late

Greater longevity

Increased parental care

Increased competition

Fewer offspring

Larger offspring

Characteristics of r -selected species

Mature early

Lower longevity

Decreased parental care

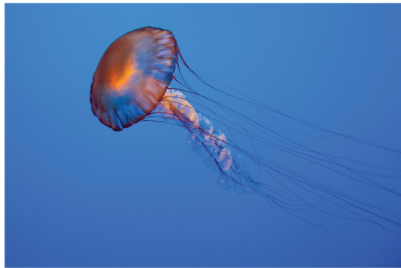
Decreased competition

More offspring

Smaller offspring



(a) K -selected species



(b) r -selected species

Modern Theories of Life History

The r - and K -selection theory, although accepted for

decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's predictions. Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New **demographic-based models** of life history evolution have been developed which incorporate many ecological concepts included in r - and K -selection theory as well as population age structure and mortality factors.

Section Summary

Populations are regulated by a variety of density-dependent and density-independent factors. Species are divided into two categories based on a variety of features of their life history patterns: r -selected species, which have large numbers of offspring, and K -selected species, which have few offspring. The r - and K -selection theory has fallen out of use; however, many of its key features are still used in newer, demographically-based models of population dynamics.

Review Questions

Species that have many offspring at one time are usually:

1. r -selected
 2. K -selected
 3. both r - and K -selected
 4. not selected
-

A

A forest fire is an example of _____ regulation.

1. density-dependent
 2. density-independent
 3. r -selected
 4. K -selected
-

B

Primates are examples of:

1. density-dependent species
2. density-independent species
3. r -selected species
4. K -selected species

Free Response

Give an example of how density-dependent and density-independent factors might interact.

If a natural disaster such as a fire happened in the winter, when populations are low, it would have a greater effect on the overall population and its recovery than if the same disaster occurred during the summer, when population levels are high.

Glossary

demographic-based population model

modern model of population dynamics
incorporating many features of the r - and K -
selection theory

density-dependent regulation

regulation of population that is influenced by
population density, such as crowding effects;
usually involves biotic factors

density-independent regulation

regulation of populations by factors that operate independent of population density, such as forest fires and volcanic eruptions; usually involves abiotic factors

interspecific competition

competition between species for resources in a shared habitat or environment

K-selected species

species suited to stable environments that produce a few, relatively large offspring and provide parental care

r-selected species

species suited to changing environments that produce many offspring and provide little or no parental care

Community Ecology

By the end of this section, you will be able to:

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

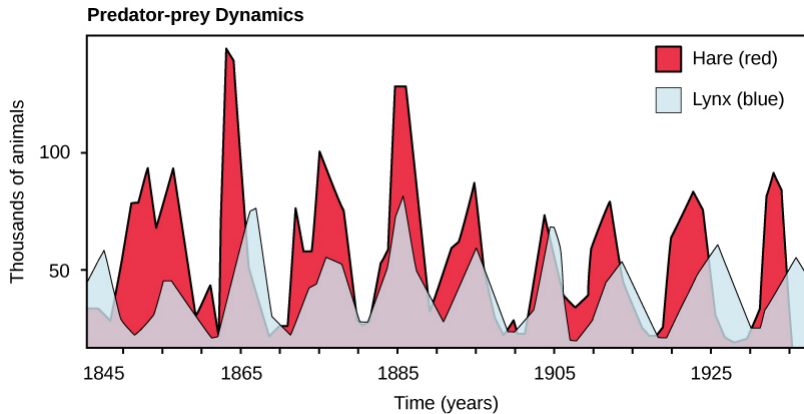
The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics. The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense,

against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by “JamieS93”/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker) (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen) (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin) Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker) Several unpleasant-tasting *Heliconius*

butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests ([link](#)). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.



The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some

plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. [\[link\]](#) shows some organisms' defenses against predation and herbivory.



(a)



(b)



(c)



(d)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs ([link]a). In another example, the chameleon can change its color to match its surroundings ([link]b). Both of these are examples of **camouflage**, or avoiding detection by blending in with the background.



Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called **aposematic coloration**, or warning coloration ([\[link\]](#)).



(a)



(b)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In **Batesian mimicry**, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation ([\[link\]](#)).



In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. [\[link\]](#) shows a variety of foul-tasting butterflies with similar coloration. In **Emsleyan/Mertensian mimicry**, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating

the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Link to Learning



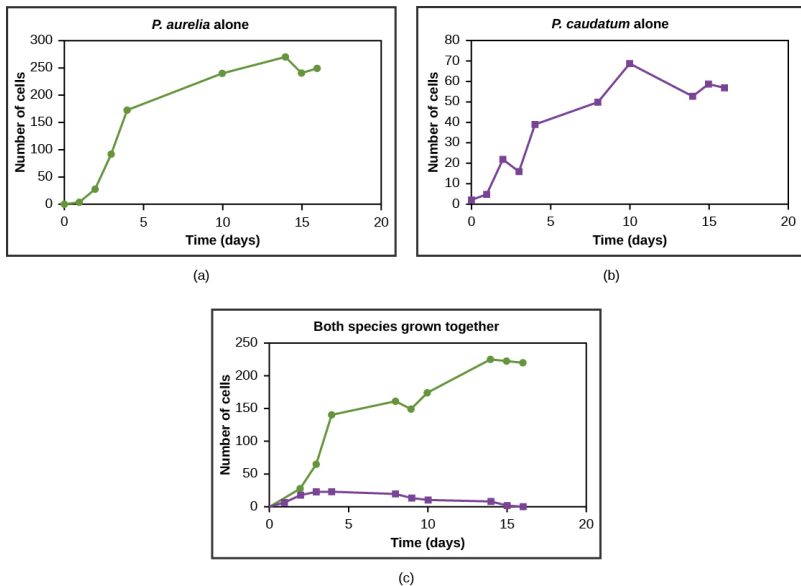
Go to this [website](#) to view stunning examples of mimicry.

Paramecium aurelia and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in [\[link\]](#), with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the

laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.



This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These organisms coexist by minimizing direct competition.

The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: “Hanay”/Wikimedia Commons) (a) Termites

form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker) This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Symbiosis

Symbiotic relationships, or **symbioses** (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship ([\[link\]](#)). The tree is not harmed by the

presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut ([\[link\]](#)a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria ([\[link\]](#)b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



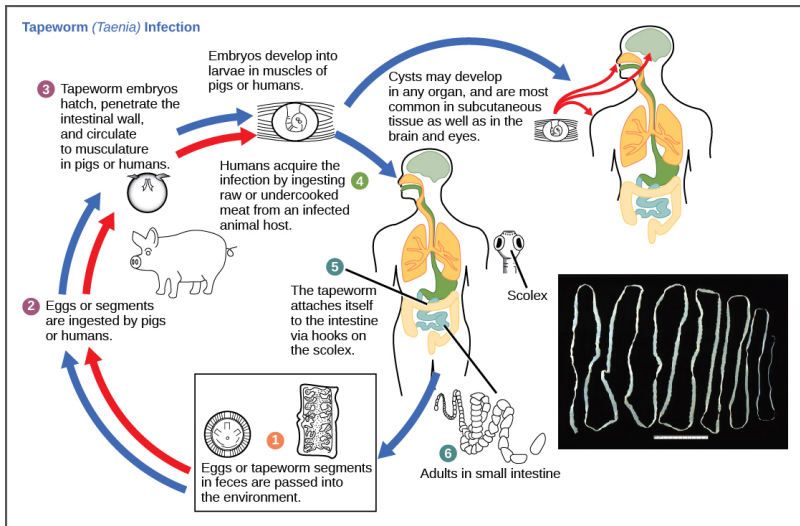
Parasitism

A **parasite** is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the **host** is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its

reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed ([\[link\]](#)). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle.

Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.



Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS) The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University) The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

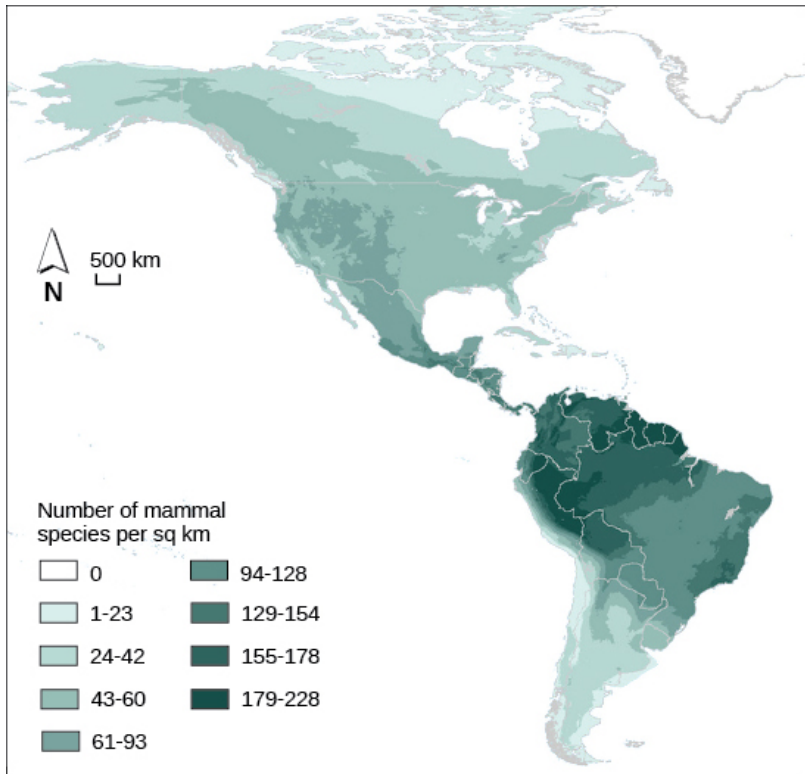
Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef ([\[link\]](#)). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.



Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. **Species richness** is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe ([\[link\]](#)). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of **island biogeography** attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. **Relative species abundance** is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.



Keystone Species

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species ([link]). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies

nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Everyday Connection

Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in [\[link\]](#). Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten

certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)



(a)



(b)



(c)



(d)



(e)



(f)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized

many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the

Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr) Secondary succession is shown in an oak and hickory forest after a forest fire.

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by **environmental disturbances** such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In **primary succession**, newly exposed or newly formed land is colonized by living things; in **secondary succession**, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as **pioneer species** ([\[link\]](#)).

These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



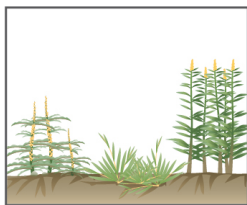
Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire ([\[link\]](#)). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life

to take hold.

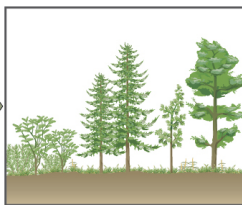
Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the **climax community**, which will remain stable until the next disturbance.

Secondary Succession of an Oak and Hickory Forest



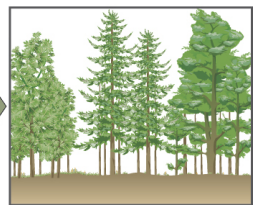
Pioneer species

Annual plants grow and are succeeded by grasses and perennials.



Intermediate species

Shrubs, then pines, and young oak and hickory begin to grow.



Climax community

The mature oak and hickory forest remains stable until the next disturbance.

Section Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Review Questions

The first species to live on new land, such as that formed from volcanic lava, are called _____.

1. climax community
 2. keystone species
 3. foundation species
 4. pioneer species
-

D

Which type of mimicry involves multiple species with similar warning coloration that are all toxic to predators?

1. Batesian mimicry
2. Müllerian mimicry
3. Emsleyan/Mertensian mimicry
4. Mertensian mimicry

B

A symbiotic relationship where both of the coexisting species benefit from the interaction is called _____.

1. commensalism
2. parasitism
3. mutualism
4. communism

C

Free Response

Describe the competitive exclusion principle and its effects on competing species.

The competitive exclusion principle states that no two species competing for the same resources at the same time and place can coexist over time. Thus, one of the competing species will eventually dominate. On the other hand, if the species evolve such that they use resources from different parts of the habitat or at different times of day, the two species can exist together indefinitely.

Glossary

aposematic coloration

warning coloration used as a defensive mechanism against predation

Batesian mimicry

type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage

avoid detection by blending in with the background.

climax community

final stage of succession, where a stable

community is formed by a characteristic assortment of plant and animal species

commensalism

relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle

no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry

type of mimicry where a harmful species resembles a less harmful one

environmental disturbance

change in the environment caused by natural disasters or human activities

foundation species

species which often forms the major structural portion of the habitat

host

organism a parasite lives on

island biogeography

study of life on island chains and how their geography interacts with the diversity of

species found there

keystone species

species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry

type of mimicry where species share warning coloration and all are harmful to predators

mutualism

symbiotic relationship between two species where both species benefit

parasite

organism that uses resources from another species, the host

pioneer species

first species to appear in primary and secondary succession

primary succession

succession on land that previously has had no life

relative species abundance

absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness

number of different species in a community

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

Ecology of Ecosystems

By the end of this section, you will be able to:

- Describe the basic types of ecosystems on Earth
- Explain the methods that ecologists use to study ecosystem structure and dynamics
- Identify the different methods of ecosystem modeling
- Differentiate between food chains and food webs and recognize the importance of each

Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material from living or previously living organisms, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical and geographic environment: a habitat's latitude, amount of rainfall, topography (elevation), and available species. These are all important environmental variables that determine which organisms can exist within a particular area.

An **ecosystem** is a community of living organisms and their interactions with their abiotic (non-living)

environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil ([link](#)).

A (a) tidal pool ecosystem in Matinicus Island in Maine is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by “takomabibelot”/Flickr; credit b: modification of work by Ivan Mlinaric)



(a)



(b)

There are three broad categories of ecosystems based on their general environment: freshwater, ocean water, and terrestrial. Within these broad categories are individual ecosystem types based on the organisms present and the type of environmental habitat.

Ocean ecosystems are the most common, comprising 75 percent of the Earth's surface and consisting of three basic types: shallow ocean, deep ocean water, and deep ocean surfaces (the low depth areas of the deep oceans). The shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, and the

deep ocean surface is known for its large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to aerobic respirators worldwide as the phytoplankton perform 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean ecosystems contain a wide variety of marine organisms. Such ecosystems exist even at the bottom of the ocean where light is unable to penetrate through the water.

Freshwater ecosystems are the rarest, occurring on only 1.8 percent of the Earth's surface. Lakes, rivers, streams, and springs comprise these systems; they are quite diverse, and they support a variety of fish, amphibians, reptiles, insects, phytoplankton, fungi, and bacteria.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories called biomes, such as tropical rain forests, savannas, deserts, coniferous forests, deciduous forests, and tundra. Grouping these ecosystems into just a few biome categories obscures the great diversity of the individual ecosystems within them. For example, there is great variation in desert vegetation: the saguaro cacti and other plant life in the Sonoran Desert, in the United States, are relatively abundant compared to the desolate rocky desert of Boa Vista, an island off the coast of Western Africa ([\[link\]](#)). Desert ecosystems, like all ecosystems, can vary

greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)



(a)



(b)

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances, or changes in the environment that effect their compositions: yearly variations in rainfall and temperature and the slower processes of plant growth, which may take several years. Many of these disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated by grasses, then by bushes and shrubs, and later by mature trees, restoring the forest to its former state. The impact of environmental disturbances caused by human activities is as important as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, eutrophication, oil spills, and illegal

dumping on land and into the ocean are all issues of concern to conservationists.

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called **resistance**. The speed at which an ecosystem recovers equilibrium after being disturbed, called its **resilience**. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon. The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level. This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows

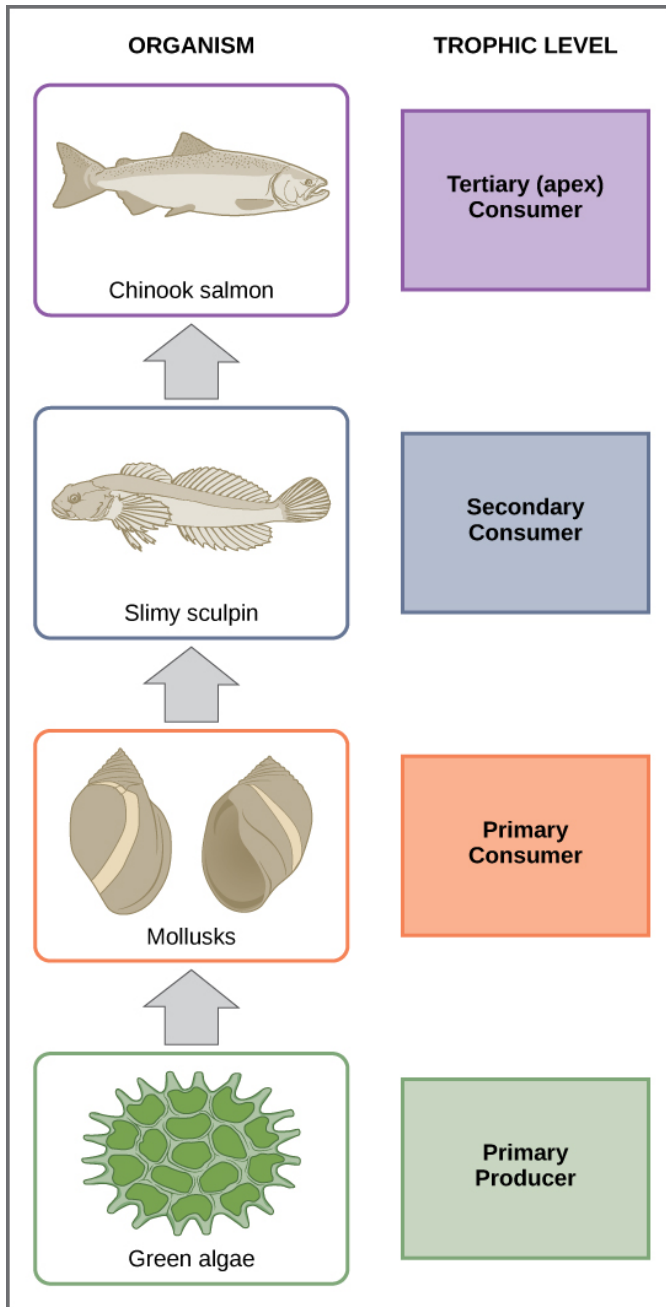
point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

Food Chains and Food Webs

The term “food chain” is sometimes used metaphorically to describe human social situations. In this sense, food chains are thought of as a competition for survival, such as “who eats whom?” Someone eats and someone is eaten. Therefore, it is not surprising that in our competitive “dog-eat-dog” society, individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

The scientific understanding of a food chain is more precise than in its everyday usage. In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain. Each organism in a food chain occupies what is called a **trophic level**. Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

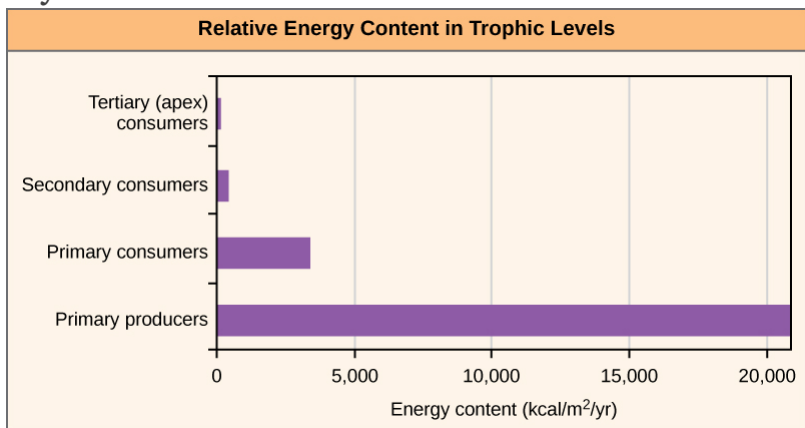
In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called **primary producers**. The organisms that consume the primary producers are herbivores: the **primary consumers**. **Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain shown in [\[link\]](#), the Chinook salmon is the apex consumer at the top of this food chain.



One major factor that limits the length of food

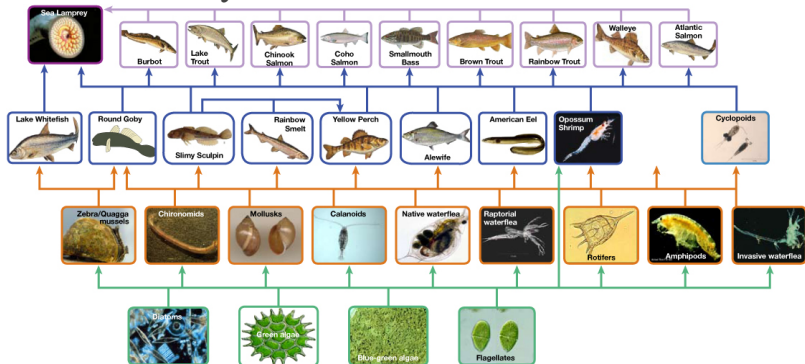
chains is energy. Energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s ([\[link\]](#)). The primary producers generated 20,819 kcal/m²/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m²/yr, the secondary consumers generated 383 kcal/m²/yr, and the tertiary consumers only generated 21 kcal/m²/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.



There is a one problem when using food chains to accurately describe most ecosystems. Even when all

organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A **food web** is a graphic representation of a holistic, non-linear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics ([\[link\]](#)).



A comparison of the two types of structural ecosystem models shows strength in both. Food chains are more flexible for analytical modeling, are easier to follow, and are easier to experiment with, whereas food web models more accurately represent ecosystem structure and dynamics, and data can be

directly used as input for simulation modeling.

Link to Learning



Head to this [online interactive simulator](#) to investigate food web function. In the *Interactive Labs* box, under Food Web, click **Step 1**. Read the instructions first, and then click **Step 2** for additional instructions. When you are ready to create a simulation, in the upper-right corner of the *Interactive Labs* box, click **OPEN SIMULATOR**.

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** (such as the Lake Ontario food web in [\[link\]](#)) has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms), called decomposers or

detritivores. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria, fungi, and detritivorous invertebrates feeding off dead plants and animals.

Evolution Conenction

Three-spined Stickleback

It is well established by the theory of natural selection that changes in the environment play a major role in the evolution of species within an ecosystem. However, little is known about how the evolution of species within an ecosystem can alter the ecosystem environment. In 2009, Dr. Luke Harmon, from the University of Idaho in Moscow, published a paper that for the first time showed that the evolution of organisms into subspecies can have direct effects on their ecosystem environment.

Footnote
Nature (Vol. 458, April 1, 2009)

The three-spines stickleback (*Gasterosteus aculeatus*) is a freshwater fish that evolved from a saltwater

fish to live in freshwater lakes about 10,000 years ago, which is considered a recent development in evolutionary time ([\[link\]](#)). Over the last 10,000 years, these freshwater fish then became isolated from each other in different lakes. Depending on which lake population was studied, findings showed that these sticklebacks then either remained as one species or evolved into two species. The divergence of species was made possible by their use of different areas of the pond for feeding called micro niches.

Dr. Harmon and his team created artificial pond microcosms in 250-gallon tanks and added muck from freshwater ponds as a source of zooplankton and other invertebrates to sustain the fish. In different experimental tanks they introduced one species of stickleback from either a single-species or double-species lake.

Over time, the team observed that some of the tanks bloomed with algae while others did not. This puzzled the scientists, and they decided to measure the water's dissolved organic carbon (DOC), which consists of mostly large molecules of decaying organic matter that give pond-water its slightly brownish color. It turned out that the water from the tanks with two-species fish contained larger particles of DOC (and hence darker water) than water with single-species fish. This increase in DOC blocked the sunlight and prevented algal blooming. Conversely, the water from the single-species tank contained smaller DOC particles,

allowing more sunlight penetration to fuel the algal blooms.

This change in the environment, which is due to the different feeding habits of the stickleback species in each lake type, probably has a great impact on the survival of other species in these ecosystems, especially other photosynthetic organisms. Thus, the study shows that, at least in these ecosystems, the environment and the evolution of populations have reciprocal effects that may now be factored into simulation models. The three-spined stickleback evolved from a saltwater fish to freshwater fish. (credit: Barrett Paul, USFWS)



Howard T. Odum, "Trophic Structure and Productivity of Silver Springs, Florida," *Ecological Monographs* 27, no. 1 (1957): 47–112.

Research into Ecosystem Dynamics: Ecosystem Experimentation and Modeling

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called **ecosystem dynamics**. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

A **holistic ecosystem model** attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is the most representative of the ecosystem in its natural state. A food web is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. To quantify all different species in an ecosystem and the dynamics in their habitat is difficult, especially when studying large habitats such as the Amazon Rainforest, which covers 1.4 billion acres (5.5 million km²) of the Earth's surface.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a

natural ecosystem that can be used for experiments, termed a **mesocosm**, or by re-creating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a **microcosm**. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environment alterations caused by partitioning (mesocosm) or re-creating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. Three basic types of ecosystem modeling are routinely used in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A

conceptual model is an ecosystem model that consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy. An **analytical model** is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. A **simulation model** is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

Conceptual Models

Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. Conceptual models are usually depicted graphically as flow charts. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. Thus, these diagrams are sometimes called compartment models.

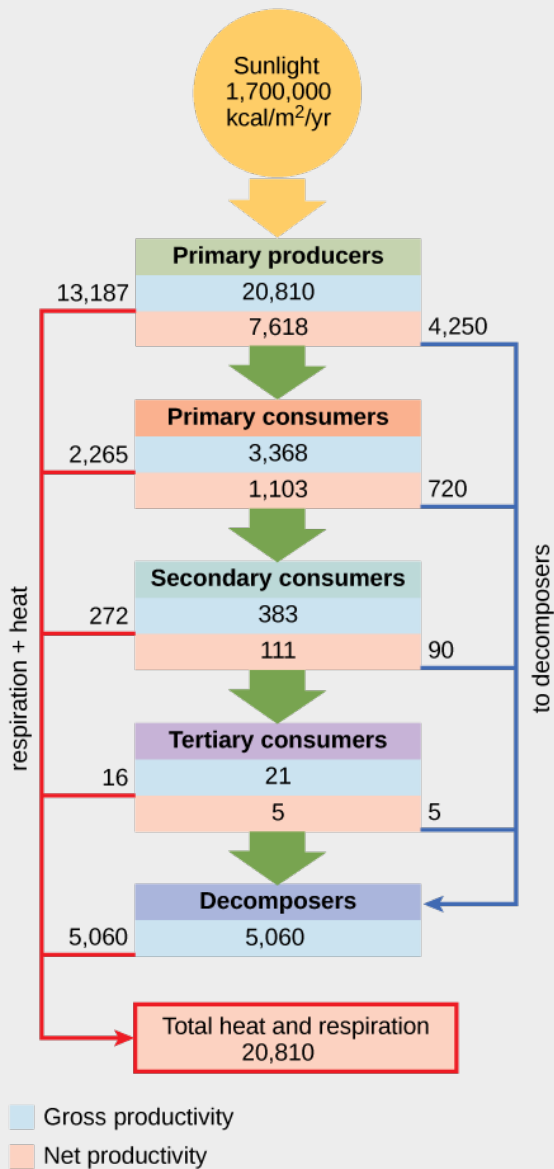
To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not. For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one. This conversion is greatly accelerated by the combustion of fossil fuels by humans, which releases large amounts of carbon dioxide into the atmosphere. This is thought to be a major factor in the rise of the atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can

use it. This process is intensified by the reduction of photosynthetic trees because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Conceptual models are also used to show the flow of energy through particular ecosystems. [\[link\]](#) is based on Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century.[\[footnote\]](#) This study shows the energy content and transfer between various ecosystem compartments.

Art Connection

This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.



Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m²/yr)?

Analytical and Simulation Models

The major limitation of conceptual models is their inability to predict the consequences of changes in ecosystem species and/or environment. Ecosystems are dynamic entities and subject to a variety of abiotic and biotic disturbances caused by natural forces and/or human activity. Ecosystems altered from their initial equilibrium state can often recover from such disturbances and return to a state of equilibrium. As most ecosystems are subject to periodic disturbances and are often in a state of change, they are usually either moving toward or away from their equilibrium state. There are many of these equilibrium states among the various components of an ecosystem, which affects the ecosystem overall. Furthermore, as humans have the ability to greatly and rapidly alter the species content and habitat of an ecosystem, the need for predictive models that enable understanding of how ecosystems respond to these changes becomes more crucial.

Analytical models often use simple, linear components of ecosystems, such as food chains, and are known to be complex mathematically; therefore, they require a significant amount of mathematical knowledge and expertise. Although analytical models have great potential, their simplification of complex ecosystems is thought to limit their accuracy. Simulation models that use computer

programs are better able to deal with the complexities of ecosystem structure.

A recent development in simulation modeling uses supercomputers to create and run individual-based simulations, which accounts for the behavior of individual organisms and their effects on the ecosystem as a whole. These simulations are considered to be the most accurate and predictive of the complex responses of ecosystems to disturbances.

Link to Learning



Visit [The Darwin Project](#) to view a variety of ecosystem models.

Section Summary

Ecosystems exist on land, at sea, in the air, and underground. Different ways of modeling ecosystems are necessary to understand how environmental disturbances will affect ecosystem structure and dynamics. Conceptual models are useful to show the general relationships between organisms and the flow of materials or energy between them. Analytical models are used to describe linear food chains, and simulation models work best with holistic food webs.

Art Connections

[\[link\]](#) Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m²/yr)?

[\[link\]](#) According to the first law of thermodynamics, energy can neither be created nor destroyed. Eventually, all energy consumed by living systems is lost as heat or used for respiration, and the total energy output of the system must equal the energy that went into it.

Review Questions

The ability of an ecosystem to return to its equilibrium state after an environmental disturbance is called _____.

1. resistance
 2. restoration
 3. reformation
 4. resilience
-

D

A re-created ecosystem in a laboratory environment is known as a _____.

1. mesocosm
 2. simulation
 3. microcosm
 4. reproduction
-

C

Decomposers are associated with which class of food web?

1. grazing

2. detrital
 3. inverted
 4. aquatic
-

B

The primary producers in an ocean grazing food web are usually _____.

1. plants
 2. animals
 3. fungi
 4. phytoplankton
-

D

What term describes the use of mathematical equations in the modeling of linear aspects of ecosystems?

1. analytical modeling
 2. simulation modeling
 3. conceptual modeling
 4. individual-based modeling
-

A

The position of an organism along a food chain is known as its _____.

1. locus
2. location
3. trophic level
4. microcosm

C

Free Response

Compare and contrast food chains and food webs. What are the strengths of each concept in describing ecosystems?

Food webs show interacting groups of different species and their many interconnections with each other and the environment. Food chains are linear aspects of food webs that describe the succession of organisms consuming one another at defined trophic levels. Food webs are a more accurate representation of the structure and dynamics of an ecosystem. Food chains are easier to model and use for experimental studies.

Describe freshwater, ocean, and terrestrial ecosystems.

Freshwater ecosystems are the rarest, but have great diversity of freshwater fish and other aquatic life. Ocean ecosystems are the most common and are responsible for much of the photosynthesis that occurs on Earth. Terrestrial ecosystems are very diverse; they are grouped based on their species and environment (biome), which includes forests, deserts, and tundras.

Compare grazing and detrital food webs. Why would they both be present in the same ecosystem?

Grazing food webs have a primary producer at their base, which is either a plant for terrestrial ecosystems or a phytoplankton for aquatic ecosystems. The producers pass their energy to the various trophic levels of consumers. At the base of detrital food webs are the decomposers, which pass this energy to a variety of other consumers. Detrital food webs are important for the health of many grazing food webs because they eliminate dead and decaying organic material, thus, clearing space for new organisms and removing potential causes of

disease. By breaking down dead organic matter, decomposers also make mineral nutrients available to primary producers; this process is a vital link in nutrient cycling.

Glossary

analytical model

ecosystem model that is created with mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics

apex consumer

organism at the top of the food chain

conceptual model

(also, compartment models) ecosystem model that consists of flow charts that show the interactions of different compartments of the living and non-living components of the ecosystem

detrital food web

type of food web in which the primary consumers consist of decomposers; these are often associated with grazing food webs within the same ecosystem

ecosystem

community of living organisms and their

interactions with their abiotic environment

ecosystem dynamics

study of the changes in ecosystem structure caused by changes in the environment or internal forces

equilibrium

steady state of an ecosystem where all organisms are in balance with their environment and each other

food chain

linear representation of a chain of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics

food web

graphic representation of a holistic, non-linear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics

grazing food web

type of food web in which the primary producers are either plants on land or phytoplankton in the water; often associated with a detrital food web within the same ecosystem

holistic ecosystem model

study that attempts to quantify the composition, interactions, and dynamics of entire ecosystems; often limited by economic and logistical difficulties, depending on the ecosystem

mesocosm

portion of a natural ecosystem to be used for experiments

microcosm

re-creation of natural ecosystems entirely in a laboratory environment to be used for experiments

primary consumer

trophic level that obtains its energy from the primary producers of an ecosystem

primary producer

trophic level that obtains its energy from sunlight, inorganic chemicals, or dead and/or decaying organic material

resilience (ecological)

speed at which an ecosystem recovers equilibrium after being disturbed

resistance (ecological)

ability of an ecosystem to remain at equilibrium in spite of disturbances

secondary consumer

usually a carnivore that eat primary consumers

simulation model

ecosystem model that is created with computer programs to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics

tertiary consumer

carnivore that eat other carnivores

trophic level

position of a species or group of species in a food chain or a food web

Energy Flow through Ecosystems

By the end of this section, you will be able to:

- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Discuss trophic levels and how ecological pyramids are used to model them

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of adenosine triphosphate, ATP), especially those responsible for building large molecules from smaller compounds, and life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

Swimming shrimp, a few squat lobsters, and

hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

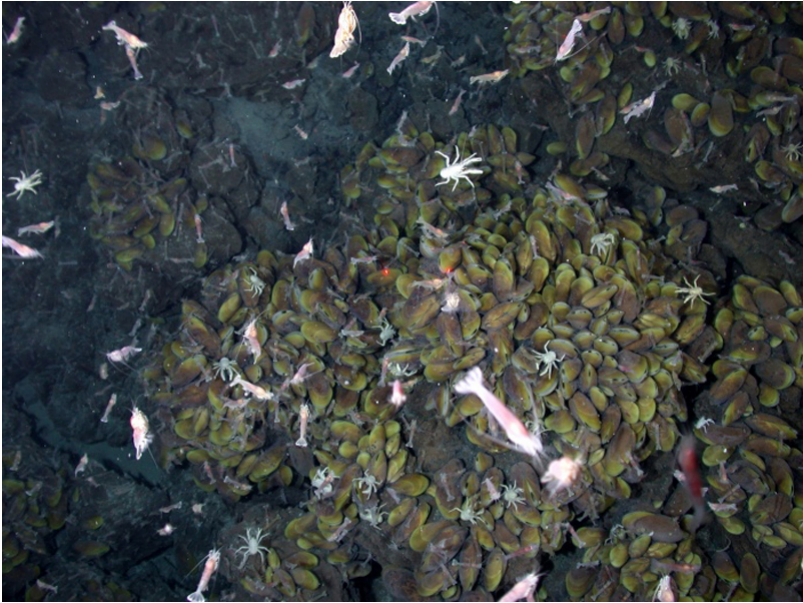
How Organisms Acquire Energy in a Food Web

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as autotrophs: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (photoautotrophs) use sunlight as an energy source, whereas chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing food webs. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean ([\[link\]](#)). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.



Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. **Biomass** is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for a biomass of 4 g/m² (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m².

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called **gross primary productivity**. An example of gross primary productivity is shown in the compartment diagram of energy flow within the Silver Springs aquatic ecosystem as shown ([\[link\]](#)). In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 kcal/m²/yr.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. **Net primary productivity** is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 kcal/m²/yr were used for respiration or were lost as heat, leaving 7,632 kcal/m²/yr of energy for use by the primary consumers.

Ecological Efficiency: The Transfer of Energy between Trophic Levels

As illustrated in [\[link\]](#), large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example ([\[link\]](#)), we see that the primary consumers produced 1103 kcal/m²/yr from the 7618 kcal/m²/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the **trophic level transfer efficiency (TLTE)** and is defined by the formula:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} \times 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. In the Lake Ontario example shown in [\[link\]](#), only three energy transfers occurred between the primary

producer, (green algae), and the apex consumer (Chinook salmon).

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. **Net production efficiency (NPE)** allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:

$$\text{NPE} = \frac{\text{net consumer productivity}}{\text{assimilation}} \times 100$$

Net consumer productivity is the energy content available to the organisms of the next trophic level. **Assimilation** is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat

only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about 1¢ to

produce 1000 dietary calories (kcal) of corn or soybeans, but approximately \$0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately \$0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Modeling Ecosystems Energy Flow: Ecological Pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. **Ecological pyramids** show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in [\[link\]](#), typical grassland during the summer has a base of many plants and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great

photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

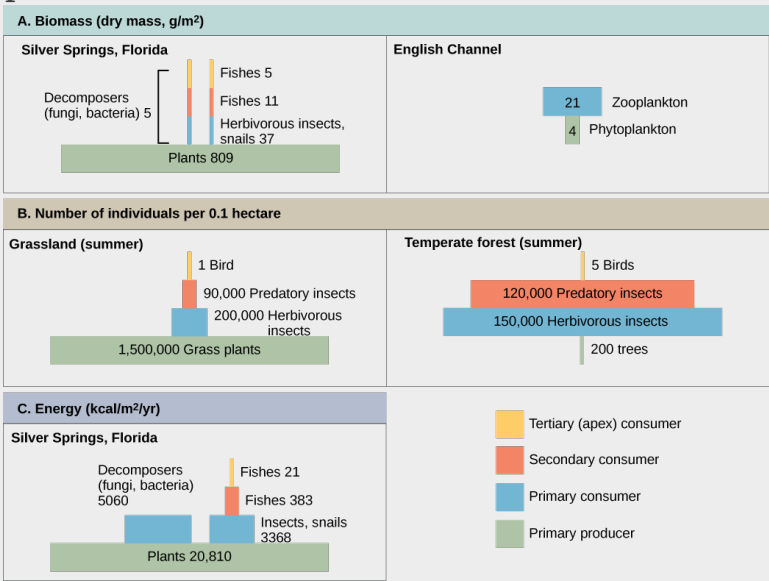
Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid ([\[link\]](#)), whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in [\[link\]](#).

Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure ([link]).

Art Connection

Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.



Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are

always upright. Why?

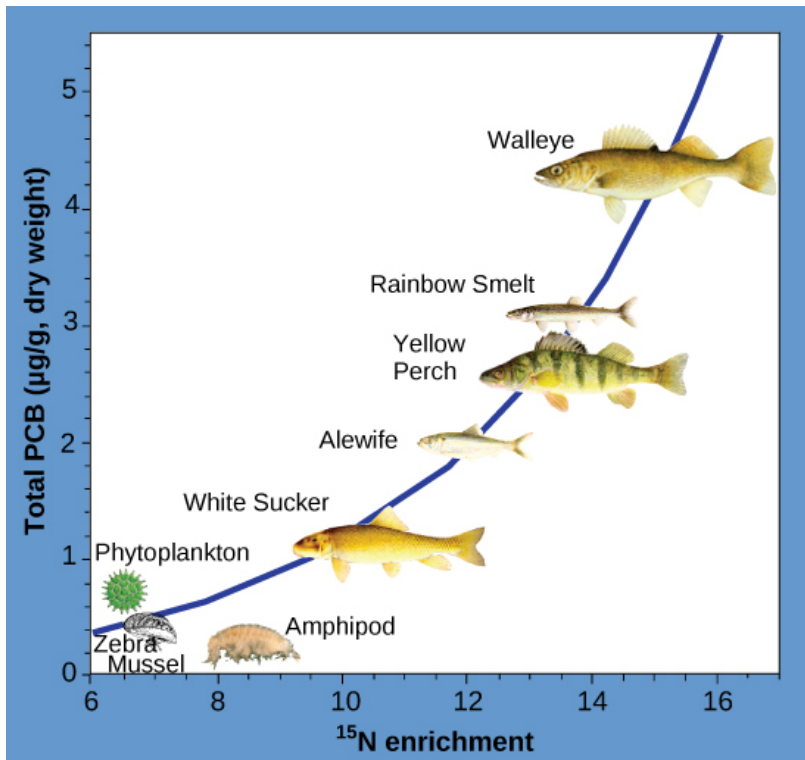
This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

Consequences of Food Webs: Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification. **Biomagnification** is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including classical studies with the pesticide **dichlorodiphenyltrichloroethane (DDT)**, which was published in the 1960s bestseller, *Silent Spring*, by Rachel Carson. DDT was a commonly used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers)

that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron ([\[link\]](#)), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.



Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant women and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Section Summary

Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. The efficiency of these transfers is important for understanding the different behaviors and eating habits of warm-blooded versus cold-blooded animals. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

Art Connections

[\[link\]](#) Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

[\[link\]](#) Pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms

reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy is always lost as heat; thus, less energy is available at each higher trophic level.

Review Questions

The weight of living organisms in an ecosystem at a particular point in time is called:

1. energy
2. production
3. entropy
4. biomass

D

Which term describes the process whereby toxic substances increase along trophic levels of an

ecosystem?

1. biomassification
 2. biomagnification
 3. bioentropy
 4. heterotrophy
-

B

Organisms that can make their own food using inorganic molecules are called:

1. autotrophs
 2. heterotrophs
 3. photoautotrophs
 4. chemoautotrophs
-

D

In the English Channel ecosystem, the number of primary producers is smaller than the number of primary consumers because_____.

1. the apex consumers have a low turnover rate
2. the primary producers have a low turnover rate
3. the primary producers have a high

- turnover rate
4. the primary consumers have a high turnover rate
-

C

What law of chemistry determines how much energy can be transferred when it is converted from one form to another?

1. the first law of thermodynamics
 2. the second law of thermodynamics
 3. the conservation of matter
 4. the conservation of energy
-

B

Free Response

Compare the three types of ecological pyramids and how well they describe ecosystem structure. Identify which ones can be inverted and give an example of an inverted pyramid for each.

Pyramids of numbers display the number of individual organisms on each trophic level. These pyramids can be either upright or inverted, depending on the number of the organisms. Pyramids of biomass display the weight of organisms at each level. Inverted pyramids of biomass can occur when the primary producer has a high turnover rate. Pyramids of energy are usually upright and are the best representation of energy flow and ecosystem structure.

How does the amount of food a warm blooded-animal (endotherm) eats relate to its net production efficiency (NPE)?

NPE measures the rate at which one trophic level can use and make biomass from what it attained in the previous level, taking into account respiration, defecation, and heat loss. Endotherms have high metabolism and generate a lot of body heat. Although this gives them advantages in their activity level in colder temperatures, these organisms are 10 times less efficient at harnessing the energy from the food they eat compared with cold-blooded animals, and thus have to eat more and more often.

Glossary

assimilation

biomass consumed and assimilated from the previous trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste

biomagnification

increasing concentrations of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers

biomass

total weight, at the time of measurement, of living or previously living organisms in a unit area within a trophic level

chemoautotroph

organism capable of synthesizing its own food using energy from inorganic molecules

ecological pyramid

(also, Eltonian pyramid) graphical representation of different trophic levels in an ecosystem based on organism numbers, biomass, or energy content

gross primary productivity

rate at which photosynthetic primary producers incorporate energy from the sun

net consumer productivity

energy content available to the organisms of the next trophic level

net primary productivity

energy that remains in the primary producers after accounting for the organisms' respiration and heat loss

net production efficiency (NPE)

measure of the ability of a trophic level to convert the energy it receives from the previous trophic level into biomass

trophic level transfer efficiency (TLTE)

energy transfer efficiency between two successive trophic levels

Biogeochemical Cycles

By the end of this section, you will be able to:

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**.

Water contains hydrogen and oxygen, which is essential to all living processes. The **hydrosphere** is the area of the Earth where water movement and

storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3-D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Link to Learning



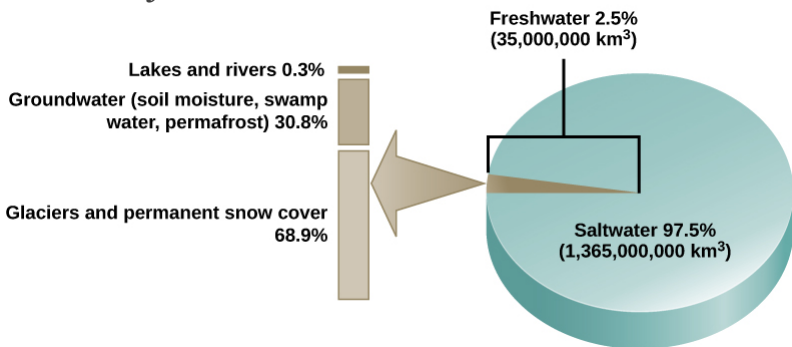
Head to this [website](#) to learn more about biogeochemical cycles.

Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things. This graph shows the average residence time for water molecules in the Earth's water reservoirs. Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on

Earth, 97.5 percent of it is non-potable salt water ([\[link\]](#)). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.



Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. [\[link\]](#) illustrates the average time that an individual water molecule

may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

Average Residence Time for Water Molecules	
Biospheric (in living organisms)	1 week
Atmospheric	1.5 weeks
Rivers	2 weeks
Soil moisture	2 weeks–1 year
Swamps	1–10 years
Lakes & reservoirs	10 years
Oceans & seas	4,000 years
Groundwater	2 weeks to 10,000 years
Glaciers and permafrost	1,000–10,000 years

There are various processes that occur during the cycling of water, shown in [\[link\]](#). These processes include the following:

- evaporation/sublimation

- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

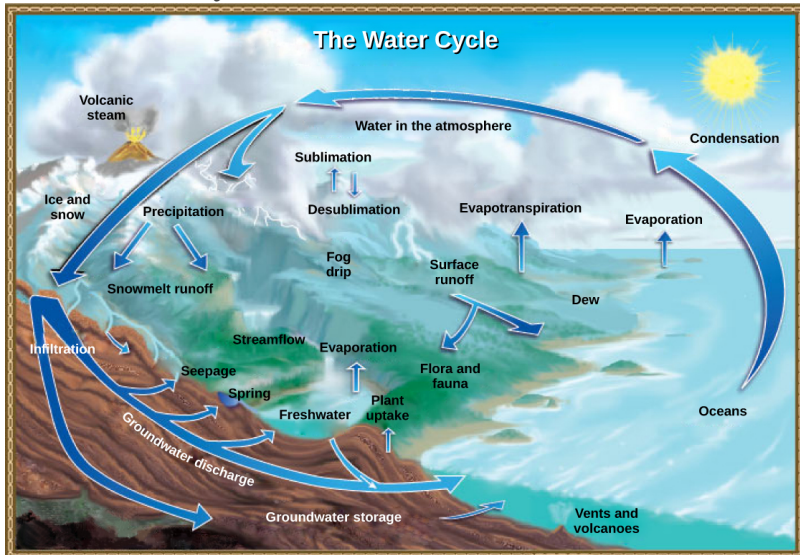
The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Link to Learning



Head to this [website](#) to learn more about the world's fresh water supply.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.



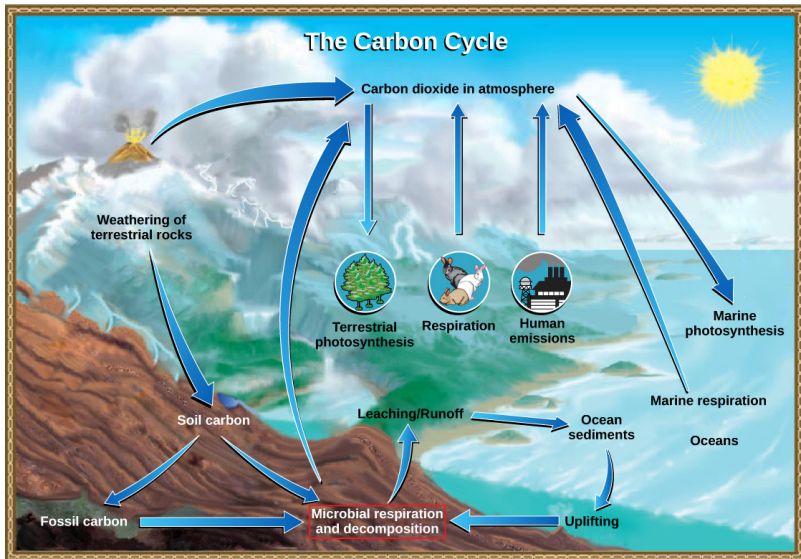
Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles

the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS) Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth's limited fossil fuel supplies has risen; therefore, the amount of carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth's ecosystems and is a major environmental concern worldwide. Thus, the "carbon footprint" is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in [\[link\]](#).



Link to Learning



Click this [link](#) to read information about the United

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, H_2CO_3). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the

autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in

each location, and each one affects the other reciprocally. Carbon dioxide (CO₂) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions ([\[link\]](#))

Step 1: CO₂ (atmospheric) \rightleftharpoons CO₂ (dissolved)

Step 2: CO₂ (dissolved) + H₂O \rightleftharpoons H₂CO₃ (carbonic acid)

Step 3: H₂CO₃ \rightleftharpoons + H⁺ + HCO₃⁻ (bicarbonate ion)

Step 4: HCO₃⁻ \rightleftharpoons H⁺ + CO₃²⁻ (carbonate ion)

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate (CaCO₃), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a non-renewable resource because their use far exceeds

their rate of formation. A **non-renewable resource**, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of **subduction**: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and the respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossil fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, "Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock," *Nature* 477, no. 7362 (2011): 78–81.

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to “fix” nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

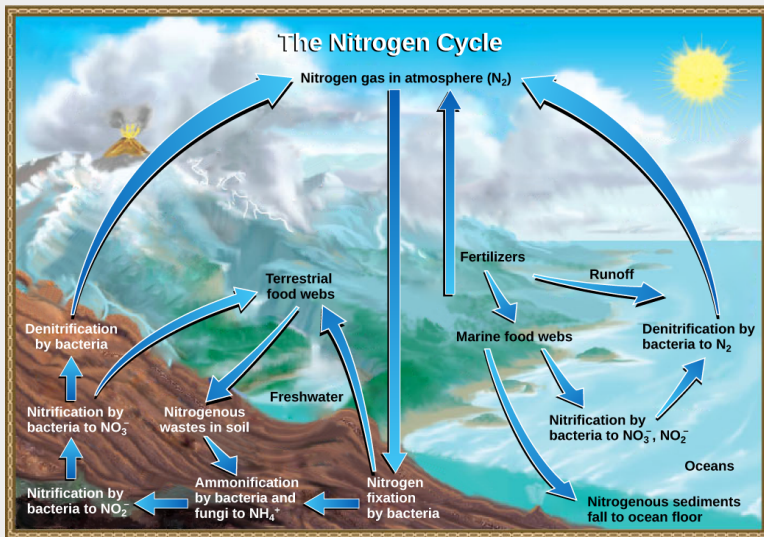
Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in [\[link\]](#), the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the

ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

Art Connection

Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)





Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in

agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle. [\[footnote\]](#)

In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate

dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS) Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

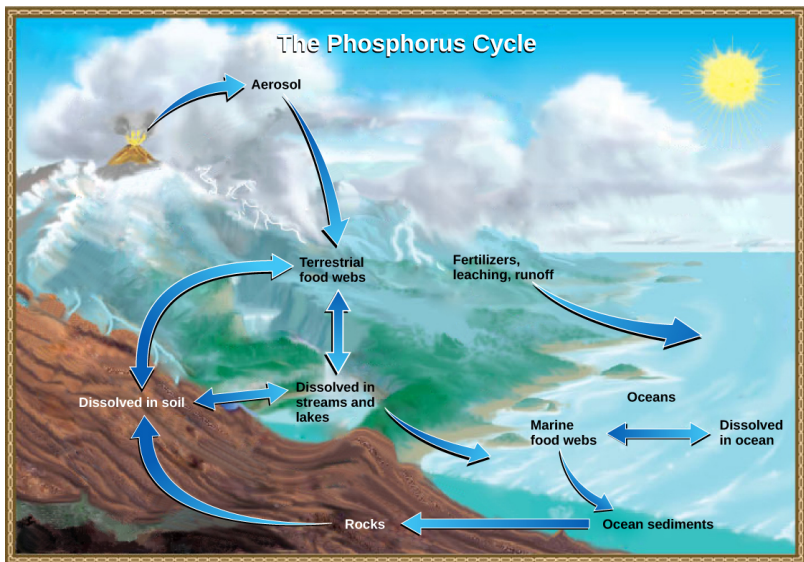
The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems ([\[link\]](#)).

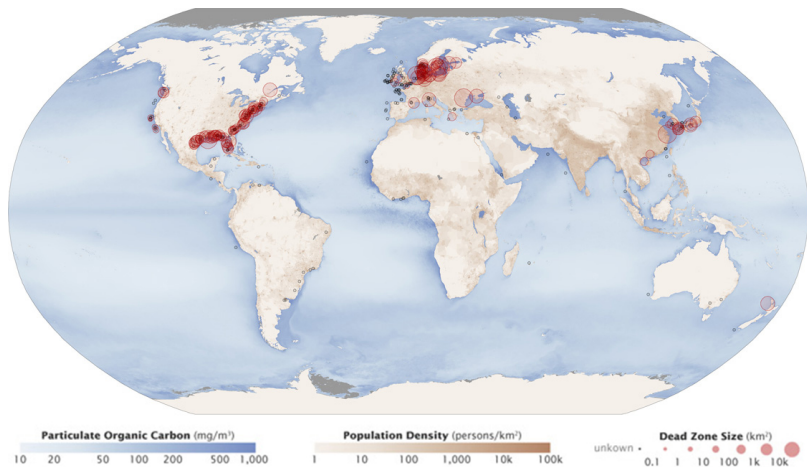
Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is

moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.



Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers ([link]).



A **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Everyday Connection
Chesapeake Bay

This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)



(a)



(b)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the

Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the

oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

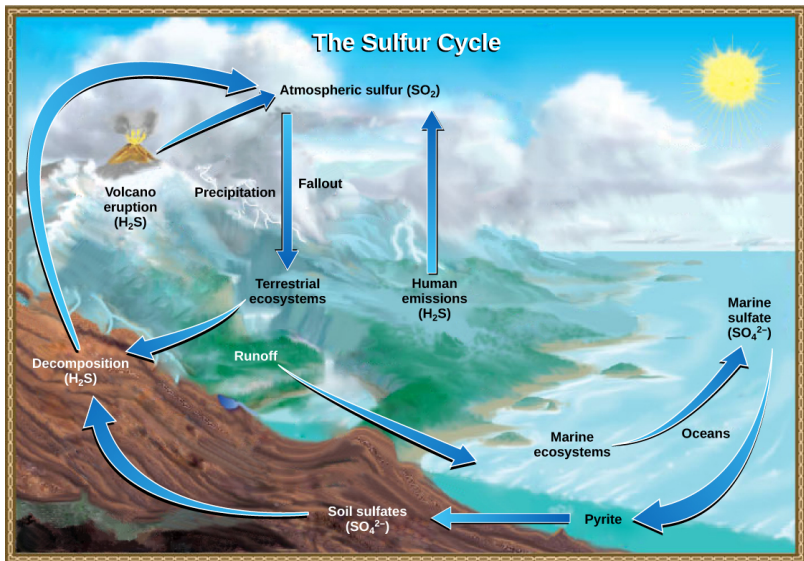
Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout.

Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS) At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in [\[link\]](#), sulfur cycles between the oceans, land, and atmosphere.

Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.



On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents ([\[link\]](#)). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called **fallout**. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{2-}), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.



Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems ([\[link\]](#)) rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. **Acid rain** is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid

rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

Link to Learning



Click this [link](#) to learn more about global climate change.

Section Summary

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. As human activities have caused major disturbances to these cycles, their study and modeling is especially important. A variety of human activities, such as pollution, oil spills, and events) have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

Art Connections

[\[link\]](#) Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

[\[link\]](#) C: Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Review Questions

The movement of mineral nutrients through organisms and their environment is called a _____ cycle.

1. biological
2. bioaccumulation
3. biogeochemical
4. biochemical

C

Carbon is present in the atmosphere as _____.

1. carbon dioxide
2. carbonate ion
3. carbon dust
4. carbon monoxide

A

The majority of water found on Earth is:

1. ice
 2. water vapor
 3. fresh water
 4. salt water
-

D

The average time a molecule spends in its reservoir is known as _____.

1. residence time
 2. restriction time
 3. resilience time
 4. storage time
-

A

The process whereby oxygen is depleted by the growth of microorganisms due to excess nutrients in aquatic systems is called _____.

1. dead zoning
 2. eutrophication
 3. retrofication
 4. depletion
-

B

The process whereby nitrogen is brought into organic molecules is called _____.

1. nitrification
2. denitrification
3. nitrogen fixation
4. nitrogen cycling

C

Free Response

Describe nitrogen fixation and why it is important to agriculture.

Nitrogen fixation is the process of bringing nitrogen gas from the atmosphere and incorporating it into organic molecules. Most plants do not have this capability and must rely on free-living or symbiotic bacteria to do this. As nitrogen is often the limiting nutrient in the growth of crops, farmers make use of artificial fertilizers to provide a nitrogen source to the

plants as they grow.

What are the factors that cause dead zones? Describe eutrophication, in particular, as a cause.

Many factors can kill life in a lake or ocean, such as eutrophication by nutrient-rich surface runoff, oil spills, toxic waste spills, changes in climate, and the dumping of garbage into the ocean. Eutrophication is a result of nutrient-rich runoff from land using artificial fertilizers high in nitrogen and phosphorus. These nutrients cause the rapid and excessive growth of microorganisms, which deplete local dissolved oxygen and kill many fish and other aquatic organisms.

Why are drinking water supplies still a major concern for many countries?

Most of the water on Earth is salt water, which humans cannot drink unless the salt is removed. Some fresh water is locked in glaciers and polar ice caps, or is present in the atmosphere. The Earth's water supplies are threatened by pollution and exhaustion. The effort to supply fresh drinking water to the planet's ever-

expanding human population is seen as a major challenge in this century.

Glossary

acid rain

corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

biogeochemical cycle

cycling of mineral nutrients through ecosystems and through the non-living world

dead zone

area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities

eutrophication

process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout

direct deposit of solid minerals on land or in

the ocean from the atmosphere

hydrosphere

area of the Earth where water movement and storage occurs

non-renewable resource

resource, such as fossil fuel, that is either regenerated very slowly or not at all

residence time

measure of the average time an individual water molecule stays in a particular reservoir

subduction

movement of one tectonic plate beneath another